EVOLUTION OF VEGETATIVE MORPHOLOGY IN COENOPTERID FERNS[1]

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ABSTRACT

Salient features of the vegetative morphology of *Clepsydropsis*, *Dineuron*, *Metadineuron*, *Diplolabis*, *Metaclepsydropsis*, *Zygopteris*, *Ankyropteris*, *Psalixochlaena*, *Tubicaulis*, *Anachoropteris*, *Apotropteris*, *Grammatopteris*, *Catenopteris*, and *Botryopteris* are summarized. Trends in xylary evolution include examples of tracheidal zonation of solid protosteles (*Diplolabis*, *Grammatopteris*), increased parenchymatization of vitalized protosteles (*Tubicaulis*, *Zygopteris*), siphonostely with and without leaf gaps (*Botryopteris*, *Anachoropteris*, and *Apotropteris*), and secondary xylem (*Zygopteris*). Simple scalariform thickenings and multiseriate scalariform bordered pitting are primitive types. A distinction in foliar and cauline anatomy occurs in the earliest well known representatives of each of the coenopterid families. Branching is dichotomous (Etapteroideae), axillary (*Ankryopteris* species), lateral (*Psalixachlaena*), and effected by shoots on fronds (*Anachoropteris*, *Botryopteris*). Circinate vernation, pinnate and planated frond divisions, and laminate pinnules occur in each family including form genera *Pecopteris*, *Sphenopteris*, and *Alloiopteris*. Vegetative morphology supports recognition of coenopterids as true ferns.

Considerations of the evolutionary changes and the significance of coenopterid ferns based on vegetative morphology are indicative of our general knowledge of coenopterids—incomplete, limited in scope, and changing. An excellent review by Eggert (1964) and a comprehensive treatment of genera of the Coenopteridales by Andrews and Bureau (1970) give an overview of the diversity and familial groups of coenopterid ferns. In this paper additional observations from more recent studies on vegetative morphology are integrated with the objectives of stressing the evolution of stelar and frond morphology, particularly branching, and to suggest that vegetative genera within the Botryopteridaceae, Anachoropteridaceae, and allied genera such as *Catenopteris* are the Paleophytic representatives of true ferns and the ancestral complex for some filicalean families. More importantly, in the context of this symposium is the objective of summarizing the salient features of vegetative fern morphology of these late Paleozoic ferns, regardless of their eventual taxonomic dispositions.

Discussions of stelar evolution and frond morphology are naturally centered on better known species of *Zygopteris*, *Ankyropteris*, *Anachoropteris*, and *Botryopteris* which provide insight for interpretations of other taxa; the mixed natural and artificial assemblages allied with these genera provide a variable basis for evolutionary suppositions, but such family groupings do bring together similar vegetative morphologies, at least to the extent that they are known. Assignments of most coenopterid genera to families based on foliar anatomy are

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[1] Appreciation is expressed to Jean Galtier, Laboratoire de Paléobotanique et Evolution des Végétaux, Montpellier, to Robert L. Dennis, Oregon State University, to Donald A. Eggert, University of Illinois at Chicago Circle, and to Manfred Barthel, Museum für Paläontologie, Berlin, for their sharing illustrative material or information. A number of illustrations included on the Anachoropteridaceae are from a joint, current study with Matthew J. Avcin, Illinois State Geological Survey. Joan M. Courvoisier and Alice A. Prickett, School of Life Sciences, University of Illinois, provided technical assistance in the preparation of this manuscript.

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ANN. MISSOURI BOT. GARD. 61: 427–461. 1974.

tentative at best as is treatment of a partially known Paleozoic plant as a particular type of coenopterid fern.

Coenopterids *are*, for the most part, *ferns* which span the late Devonian through Permian time between the recognizable beginnings of fern-like morphology and the earliest-appearing extant filicalean familes (Gleicheniaceae and Osmundaceae). The tendency to assign fern-like Devonian plants as well as problematic genera such as *Stauropteris* and *Rhabdoxylon* to the Coenopteridales should not obscure the basic fern characters of the coenopterids as a whole. When Seward (1910) proposed recognition of the Coenopterideae for apparently generalized (common) Paleozoic ferns which differed from existing genera of the Filicales (and from the Marattiales), the recognition of Paleozoic pteridosperms was at hand, and real doubt existed concerning identification of the true ferns of the Carboniferous.

Each of the higher taxa represented by *Zygopteris*, *Ankyropteris*, *Botryopteris* and *Anachoropteris*, respectively, extend into the Permian. The earliest stratigraphic appearances of zygopterid ferns are probably the isolated phyllophores of *Clepsydropsis* in the Upper Devonian of Thuringia (East Germany), and genera considered here include the Mississippian *Metaclepsydropsis*, *Diplolabis*, *Clepsydropsis*, *Metadineuron*, and *Dineuron* and the Pennsylvanian-Permian *Zygopteris* assemblages. The Botryopteridaceae include *Botryopteris* with ten species; the oldest is *B. antiqua* from the Visean (Mississippian) of Scotland and France. The earliest appearance of the Anachoropteridaceae is the Westphalian A of western Europe. Among the vegetative genera considered here in the Anachoropteridaceae are *Psalixochlaena*, *Anachoropteris*, *Tubicaulis*, and *Apotropteris*. *Ankyropteris*, *Grammatopteris*, and *Catenopteris* are also discussed.

In general, the Mississippian Period seems to have been the most formative period of coenopterid vegetative evolution and diversification. Such an interpretation is based largely on the comparative morphology of Visean forms with those from the lower Westphalian A (Great Coal-Ball Horizon) of western Europe. The zygopterids with earlier geologic occurrences in the Devonian and early Mississippian seem to have evolved a specialized frond morphology and vitalized protosteles early in the Mississippian. By contrast, the Botryopteridaceae represented only by the Visean age *Botryopteris antiqua* and a species of *Grammatopteris* (*G. bertrandii*) described by Corsin (1937) from France are contemporaries with diverse zygopterid genera; by early Westphalian A time there are distinct phyletic lines of *Botryopteris*, several morphological lines of *Anachoropteris* and *Tubicaulis*, and numerous other coenopterid genera. The time gap between known Visean ferns and those of the Westphalian A apparently presents a major hiatus in the evolution of laminate foliage in coenopterids. Considerable diversification of coenopterids occurred in late Mississippian and early Pennsylvanian times, continuing into the middle Pennsylvanian. Additional genera appear in the Upper Pennsylvanian (Stephanian).

FERN MORPHOLOGY

Coenopterids are, with some exceptions, true ferns with megaphyllous leaves, foliar-borne sporangia, adventitious root systems, and circinate vernation. Cauline anatomy is typically protostelic with the occurrence of a siphonostele as early as the Westphalian A–B boundary and with several siphonostelic forms in the Middle and Upper Pennsylvanian. Secondary xylem occurs in *Zygopteris* (Dennis, 1972). Roots are typically diarch. Uniseriate multicellular hairs occur in all groups, and zygopterid ferns exhibit branched, vascularized, flattened appendages called aphlebiae on stems and/or fronds and in some cases prominent scales or long spine-like hairs. Foliar members have bilateral symmetry (with a second lateral plane of symmetry in zygopterid phyllophores); laminate foliage is probably the rule rather than the exception in Pennsylvanian time, and the evolutionary development of laminate foliage probably had occurred in all such groups by early to middle Pennsylvanian time. Circinate vernation occurs in each of the basic frond types (anachoropterid, botryopterid, and zygopterid).

Several vegetative features have characterized the coenopterids as primitive and/or different from modern ferns and have somewhat confusedly become part of the traditional concept of coenopterids in general. These are the supposed lack of distinction between stem and frond, the peculiar geometrical shapes of and/or orientations of petiolar traces (foliar xylem), and the multiseriate scalariform to elliptical and circular bordered pitting.

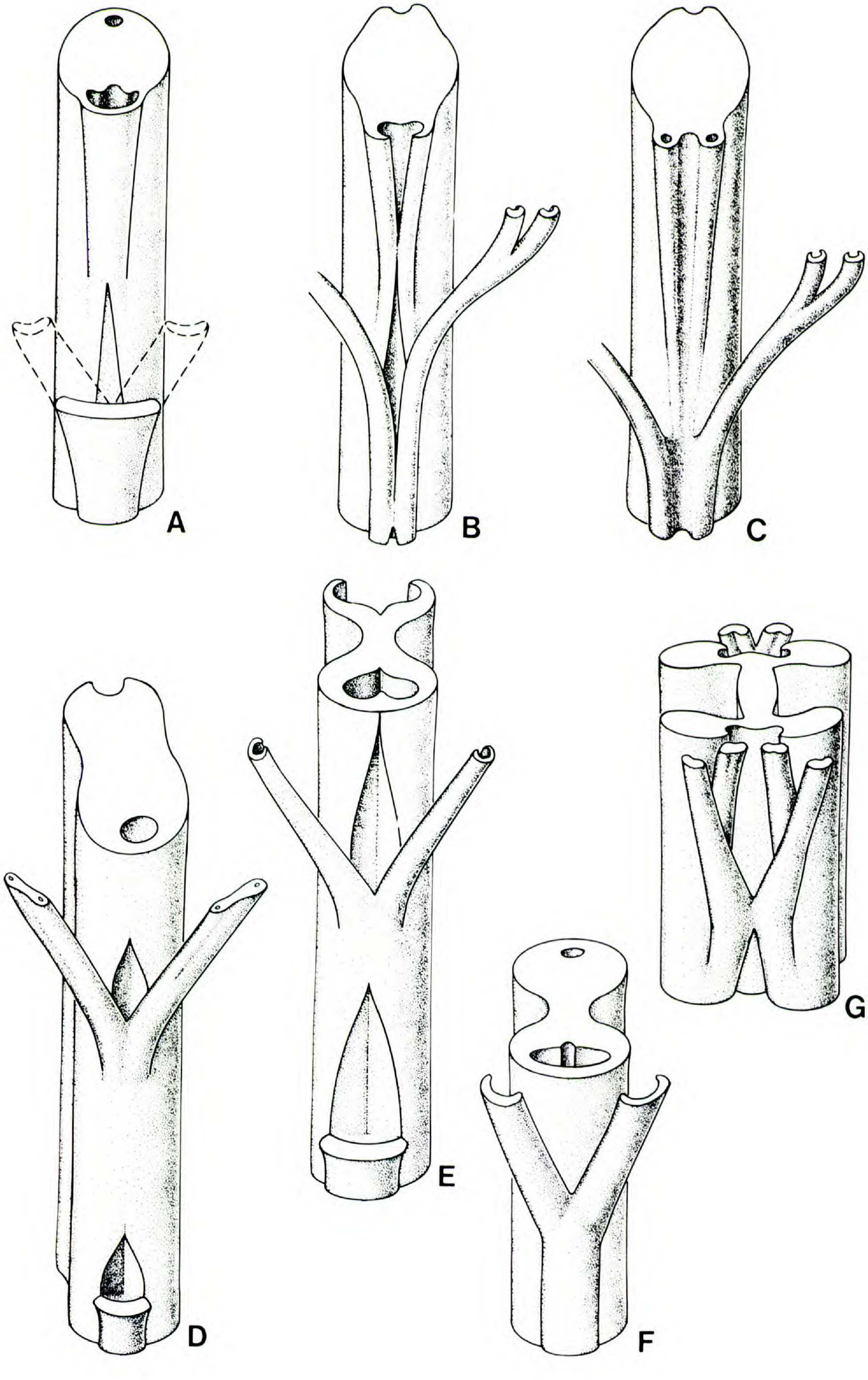
At this point the heterogeneity of coenopterids must be emphasized because the frond morphology differs markedly between zygopterid-types and those of the Botryopteridaceae and Anachoropteridaceae. The last two families seem to embody the generalized vegetative anatomy (and sporangial morphology) to consider seriously as filicalean; the zygopterid ferns constitute the largest group and for the most part seem to become quite specialized and sufficiently distinct as to warrant recognition at the ordinal level.

Anatomy of Foliar Members

The systematic use of cross-sectional foliar (non-laminate) anatomy led to initial grouping of most coenopterids into families and lower ranks, because foliar members are the common anatomically identifiable portions. Emphasis on anatomy retarded the recognition of coenopterid compressions, although numerous fertile compressions of zygopterids have been identified by means of sporangial morphology (also see Nemejc, 1936).

The basic C-shaped configuration of cross-sectional foliar xylem characterizes most ferns, with an adaxial opening in the C in practically all ferns except those of the Anachoropteridaceae in which the C is inverted (inversicatenalean). Consequently, a variety of inversicatenalean forms have been grouped with *Anachoropteris* to form the Anachoropteridaceae. The protoxylary groups of such foliar strands are adaxial and/or lateral as in catenalean types, and too much emphasis has been placed simply on inverted vascular configurations. The *Anachoropteris-Tubicaulis* complex of species seems to share numerous vegetative similarities with *Botryopteris*, and whether these reflect parallel or convergent evolution is not clear.

The Botryopteridaceae evolved the basic C-shaped foliar xylem, oriented as in modern ferns (catenalean), with an attached median xylary arm effecting an omega cross-sectional shape in several species of *Botryopteris*. Since the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monotypic Botryopteridaceae are the only family of coenopterid ferns with catenalean petiolar xylary configurations, similar C-shaped foliar types may be added to the family, such as *Catenopteris simplex*, but genera such as *Grammatopteris* and *Catenopteris* are treated herein as a separate artificial group.

ZYGOPTERIDACEAE

Significant recent studies have been completed on the vegetative morphology of zygopterid ferns from the Lower Carboniferous of France (Galtier, 1963, 1964, 1966*a*, *b*, 1970), from the Pennsylvanian of the U.S.A. (Dennis, 1972), and from the Lower Permian of East Germany (Barthel, 1968, 1970). These contributions have been emphasized in the discussion of vegetative morphology.

The zygopterid ferns include considerable diversity of form, and because of the paucity of stems among the late Devonian and Mississippian genera, the anatomy and branching of foliar members have been used to subdivide the family. The rachis of zygopterid ferns is commonly referred to as a phyllophore (Fig. 1), emphasizing its different anatomy from the typical C-shaped vascular strand of ferns and its somewhat axial relationship to the pinnae and their adaxial orientation toward it. Phyllophores exhibit lateral parenchymatous zones (peripheral loops) adjacent to protoxylem. Peripheral loops (Fig. 7) are entirely or partially surrounded by xylem. Pinna traces depart from the lateral xylary areas of peripheral loops as ring-shaped or crescent-shaped strands (Figs. 5, 8) which in turn have lateral traces (Fig. 6). Two frond morphologies separate the Clepsydroideae and Etapteroideae. Phyllophore xylem of the Clepsydroideae is typically hour-glass–shaped in cross-section and bears a row of alternating pinnae on each side; peripheral loops remain closed (permanent) in pinna formation, and metaxylem tracheids of members exhibit simple scalariform pitting. In the Etapteroideae phyllophore xylem strands range in cross-sectional shape from the simple ellipsoidal forms, *Metadineuron* and *Dineuron* (Figs. 1A–C, 2, 3), to the clepsydroid outlines of *Diplolabis* and *Metaclepsydropsis* (Fig. 1E–F, 5, 7). The H-shape of *Etapteris* (Fig. 1G, 9–10) relates geometrically as a bar with adaxial and abaxial arms or antennae which constitute a radial expansion from a clepsydroid configuration, without increase in size of the peripheral loops. Phyllophores of the Etapteroideae have temporary peripheral loops with extensive openings at pinna emission; fronds are quadriseriate with two rows of laterally borne pinnae on each side. Pinna emission usually involves a common trace at some stage of each pinna-pair, and traces show C-shaped curvature. Metaxylem tracheids have multiseriate scalariform or circular bordered pitting.

Further branching of zygopterid fronds is not well documented anatomically,

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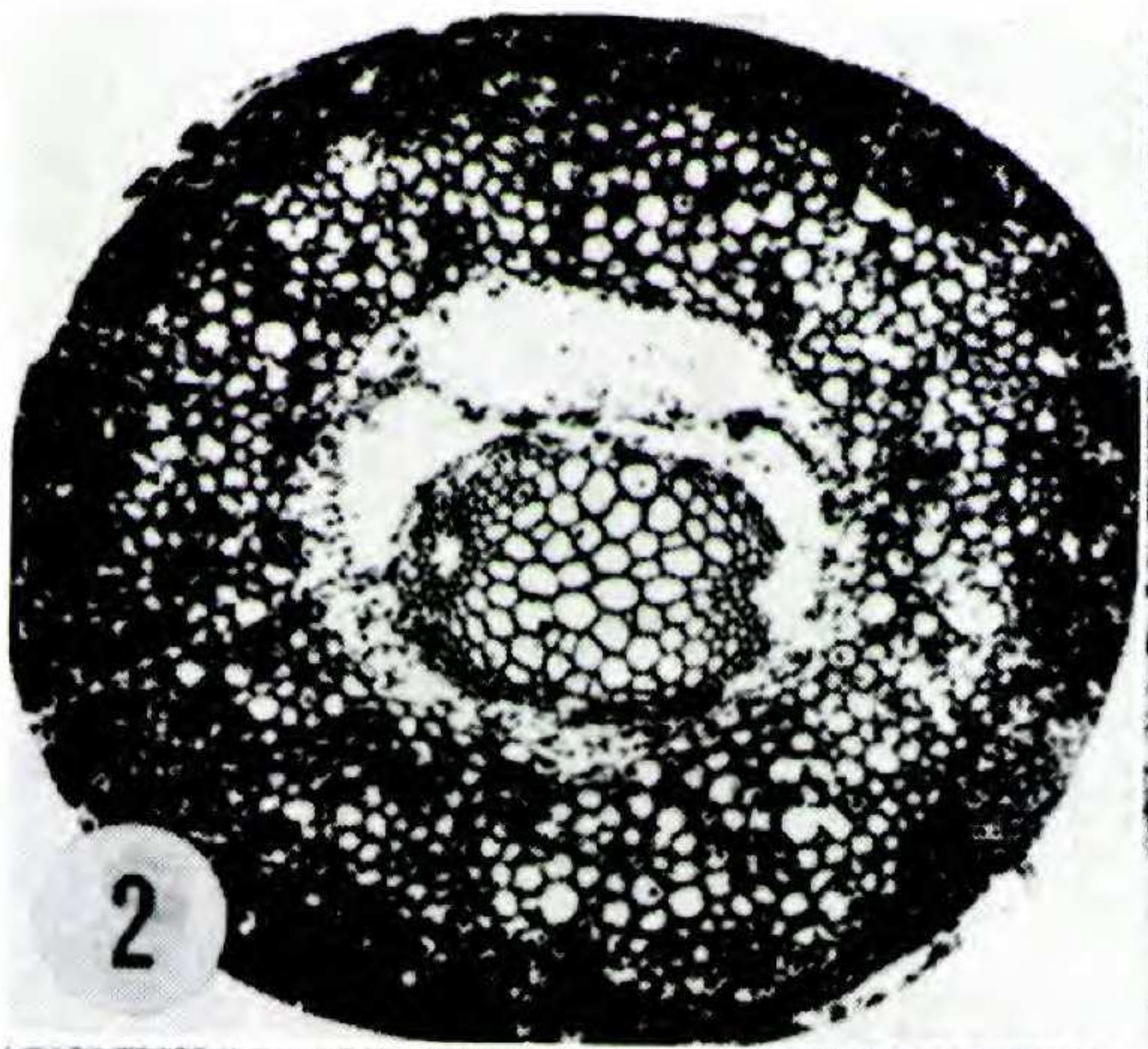
FIGURE 1. Xylary reconstructions of phyllophore (rachis) branching in "zygopterid" ferns.—A. *Metadineuron ellipticum*.—B–C. *Dineuron pteroides* alpha and beta (A–C redrawn from Galtier, 1964).—D. *Rhacophyton zygopteroides* (redrawn from Leclercq, 1951).—E. *Diplolabis roemeri*.—F. *Metaclepsydropsis duplex*.—G. *Etapteris scottii* (E–G redrawn from Posthumus, 1924).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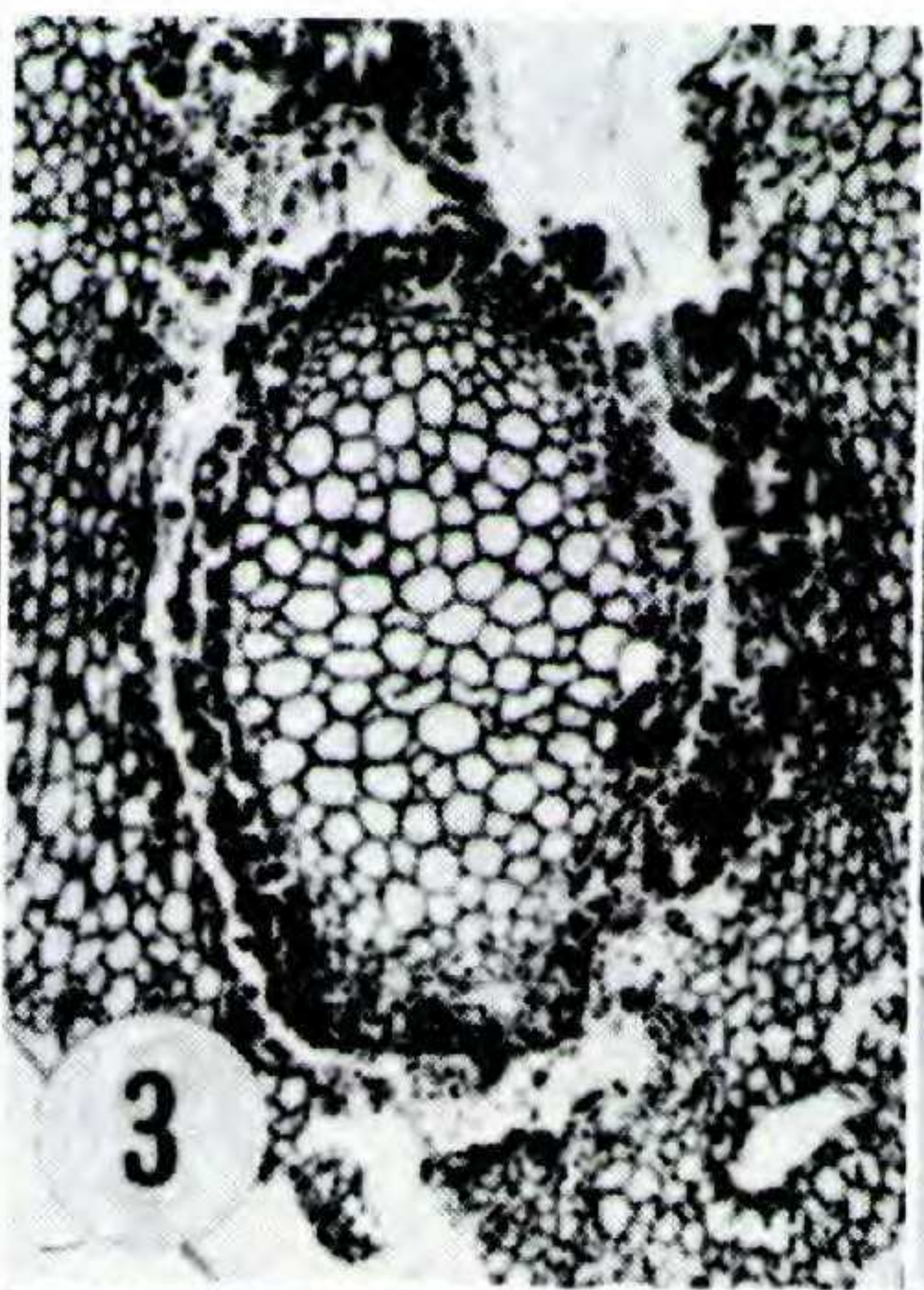
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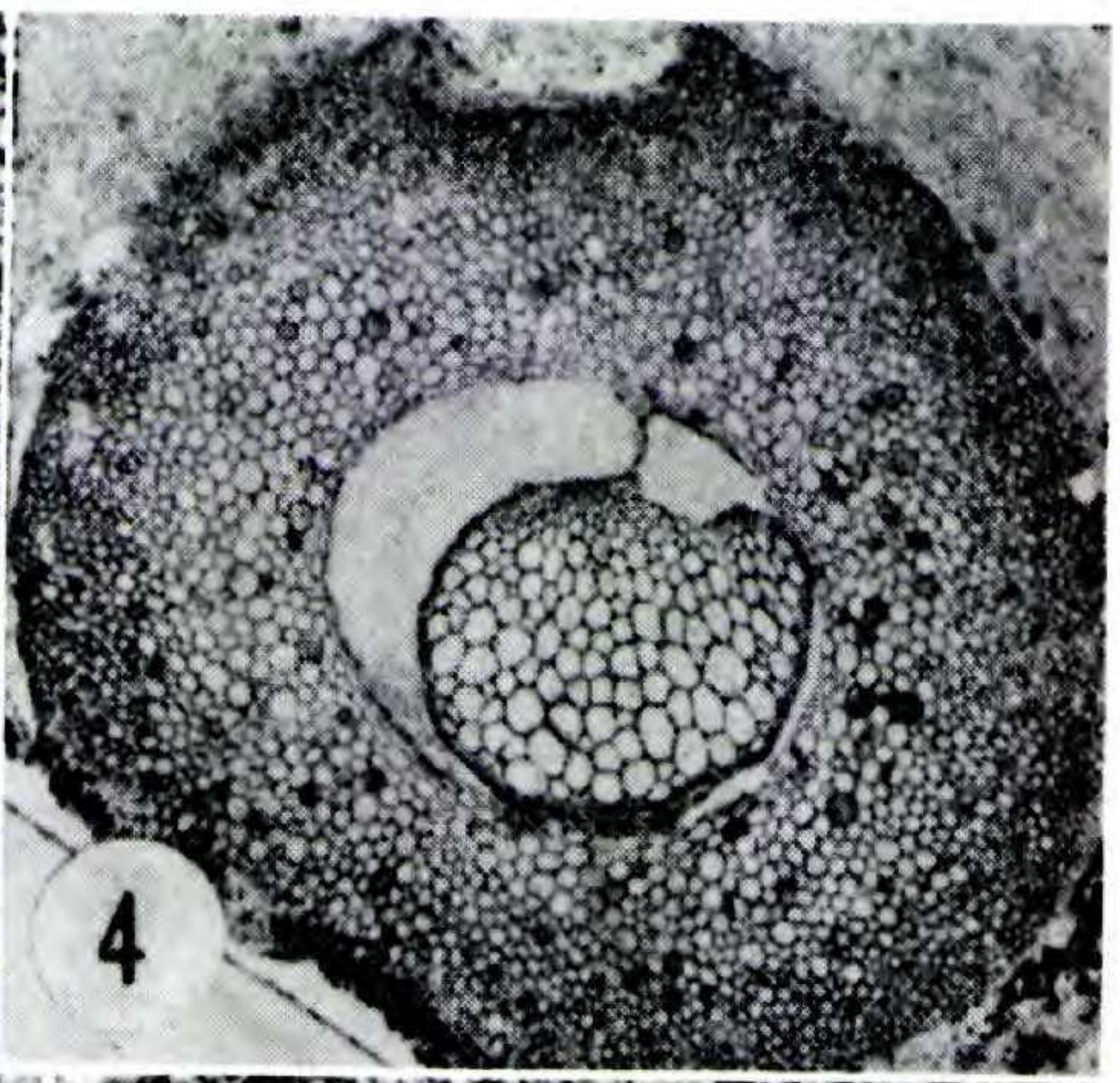
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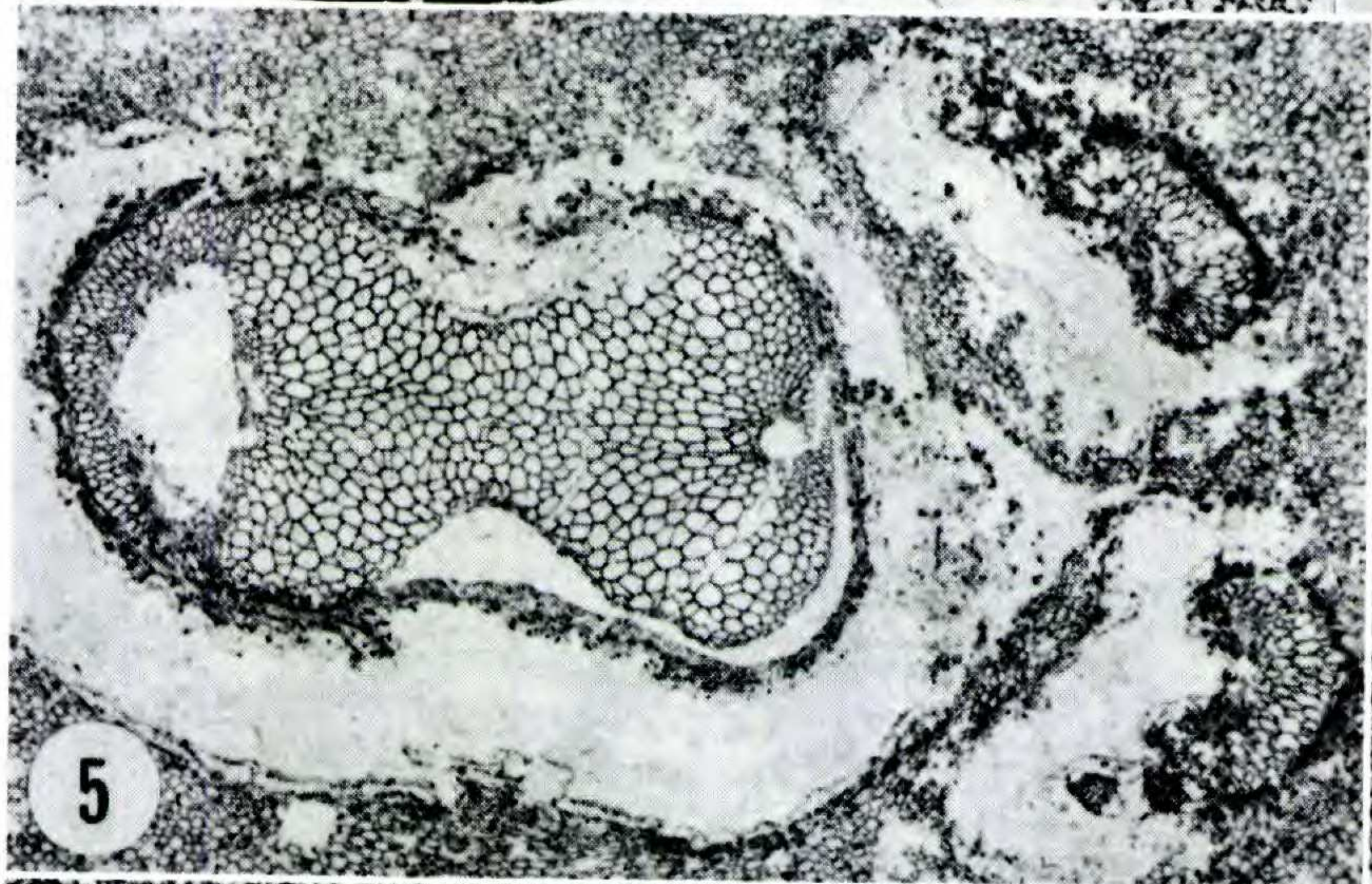
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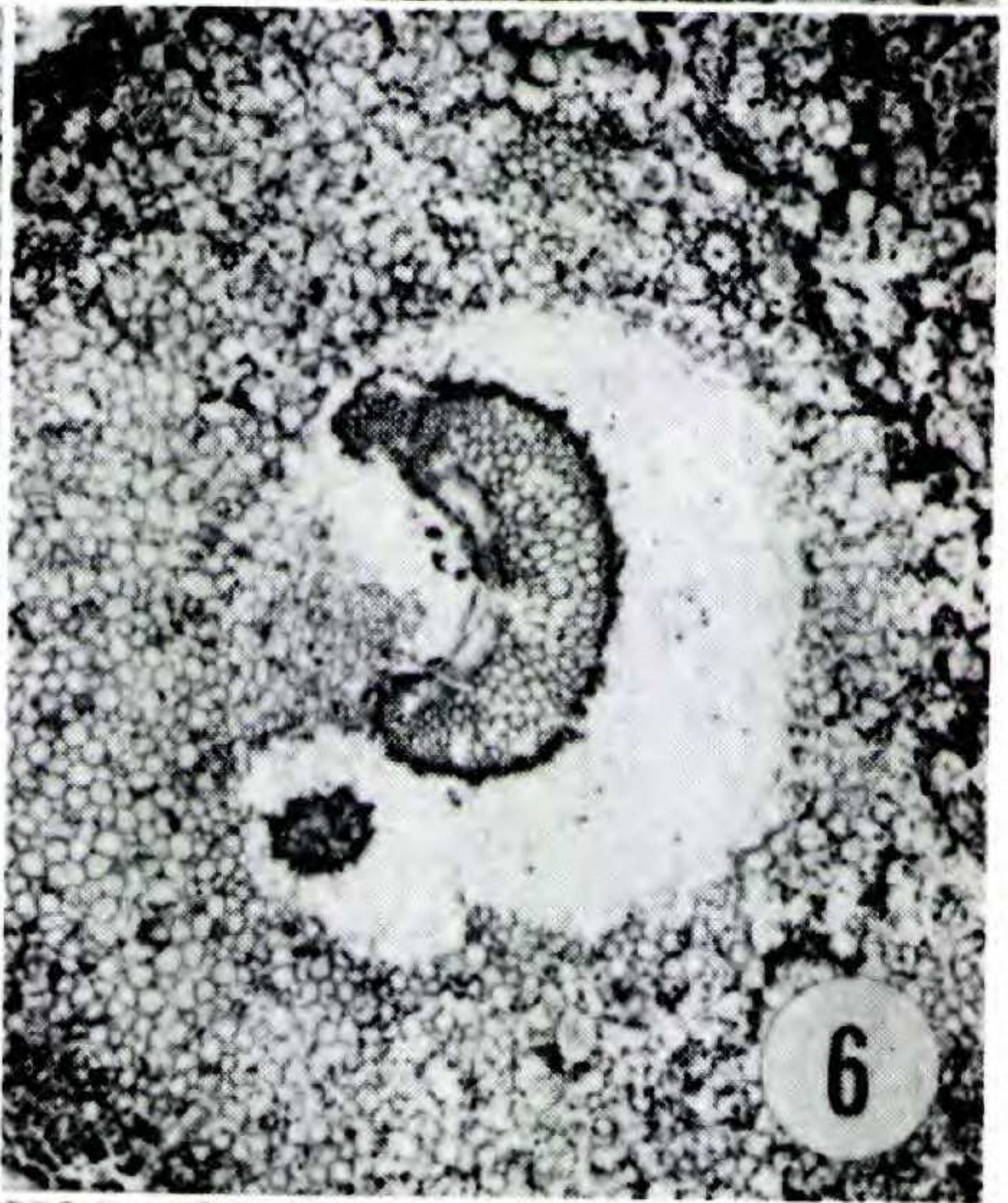
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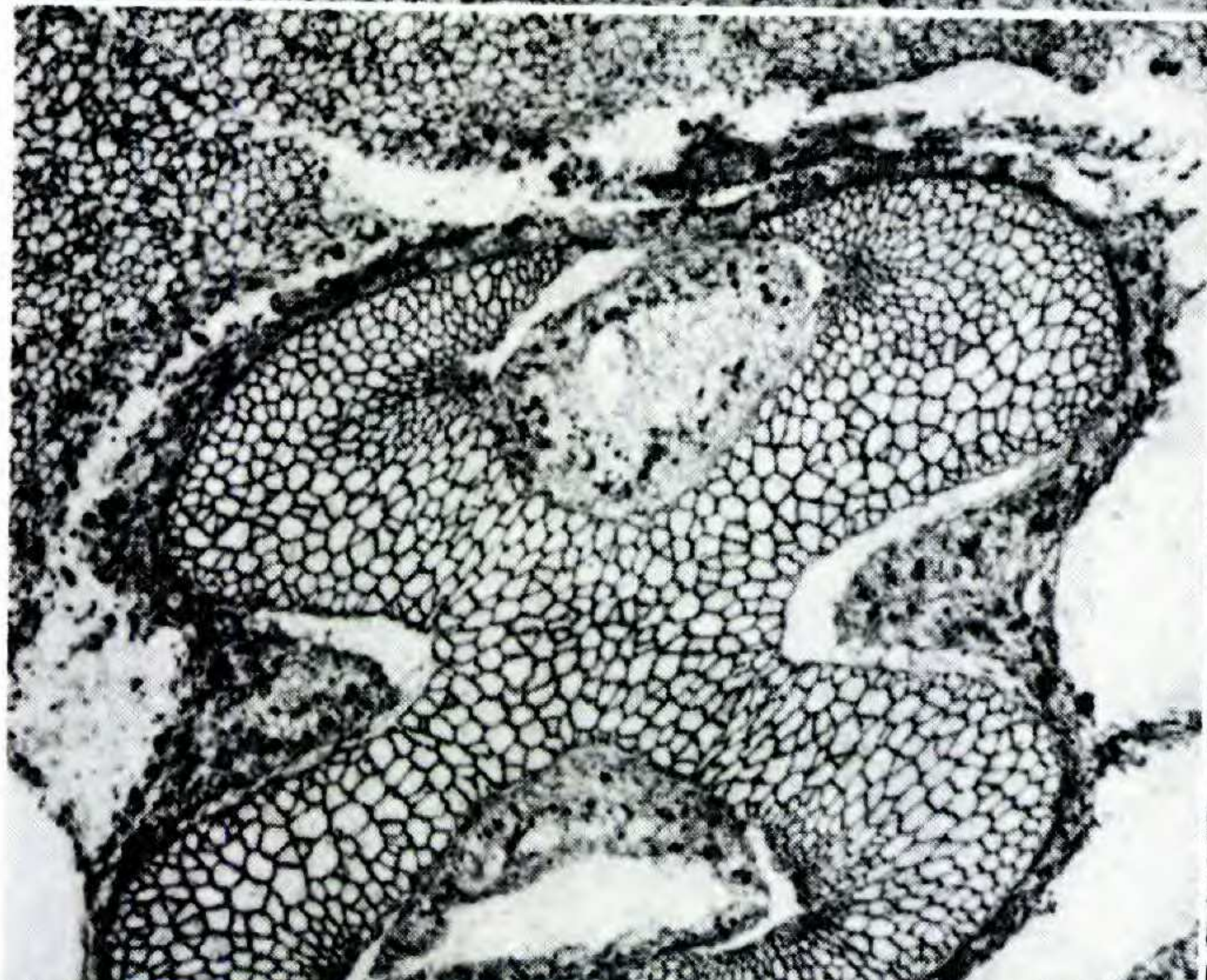
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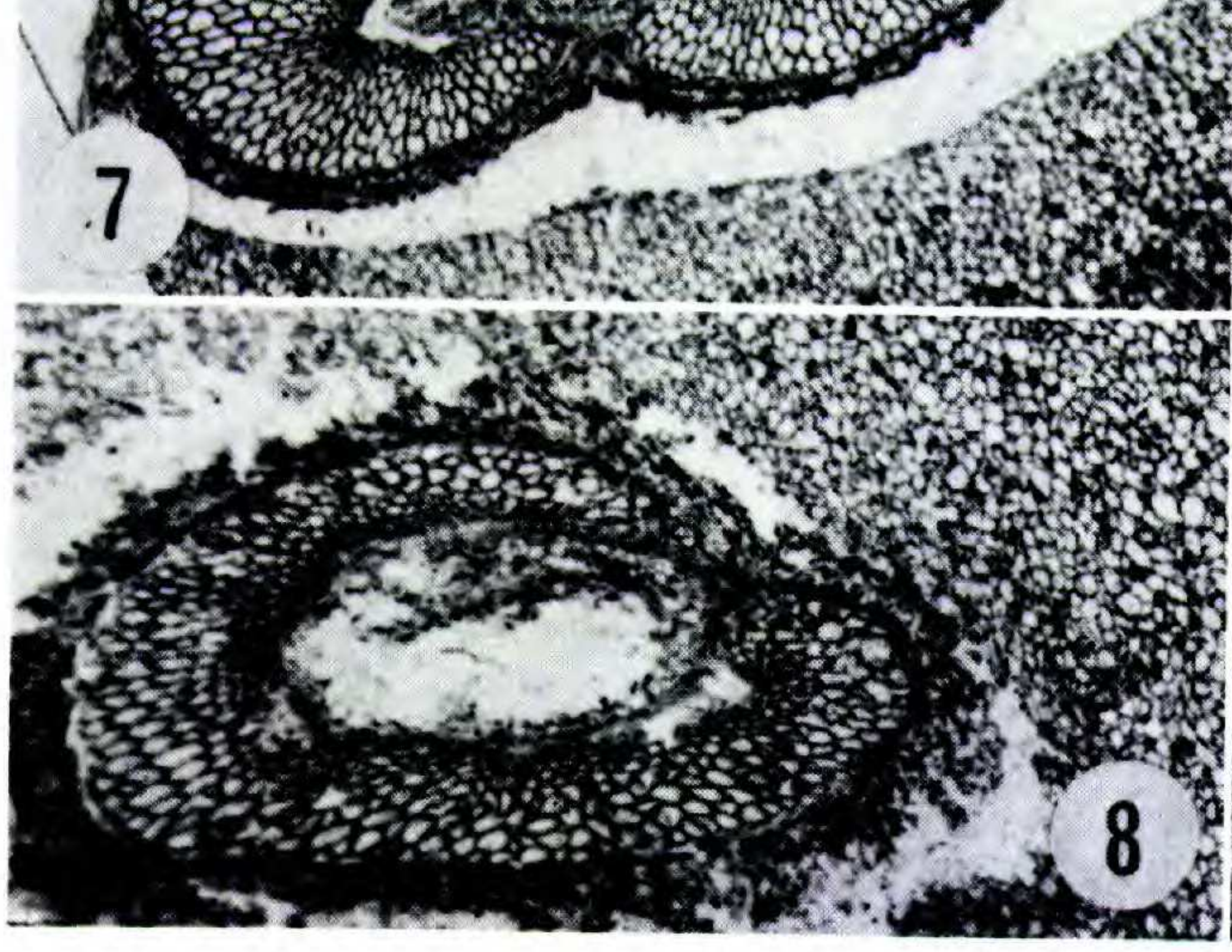
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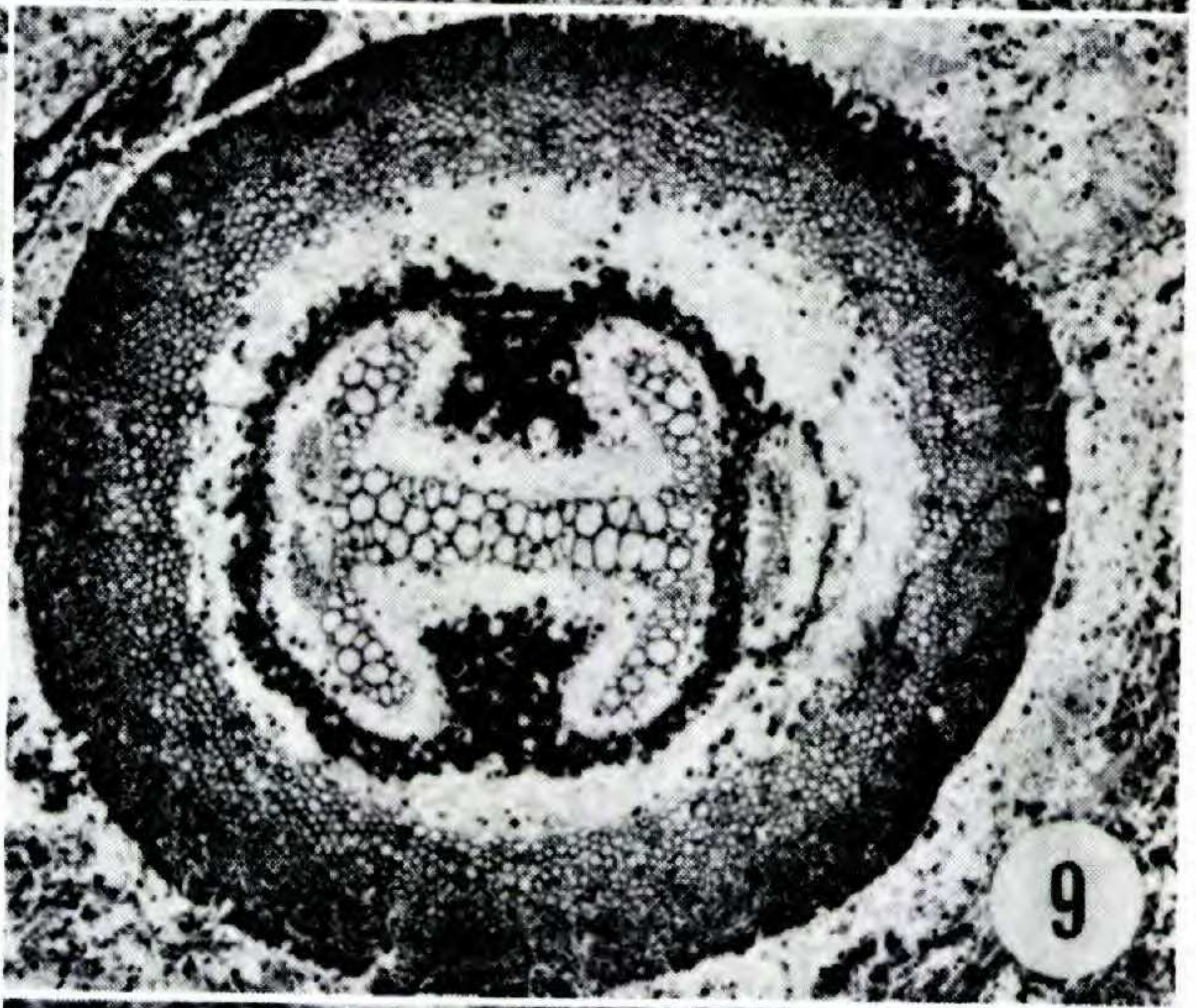
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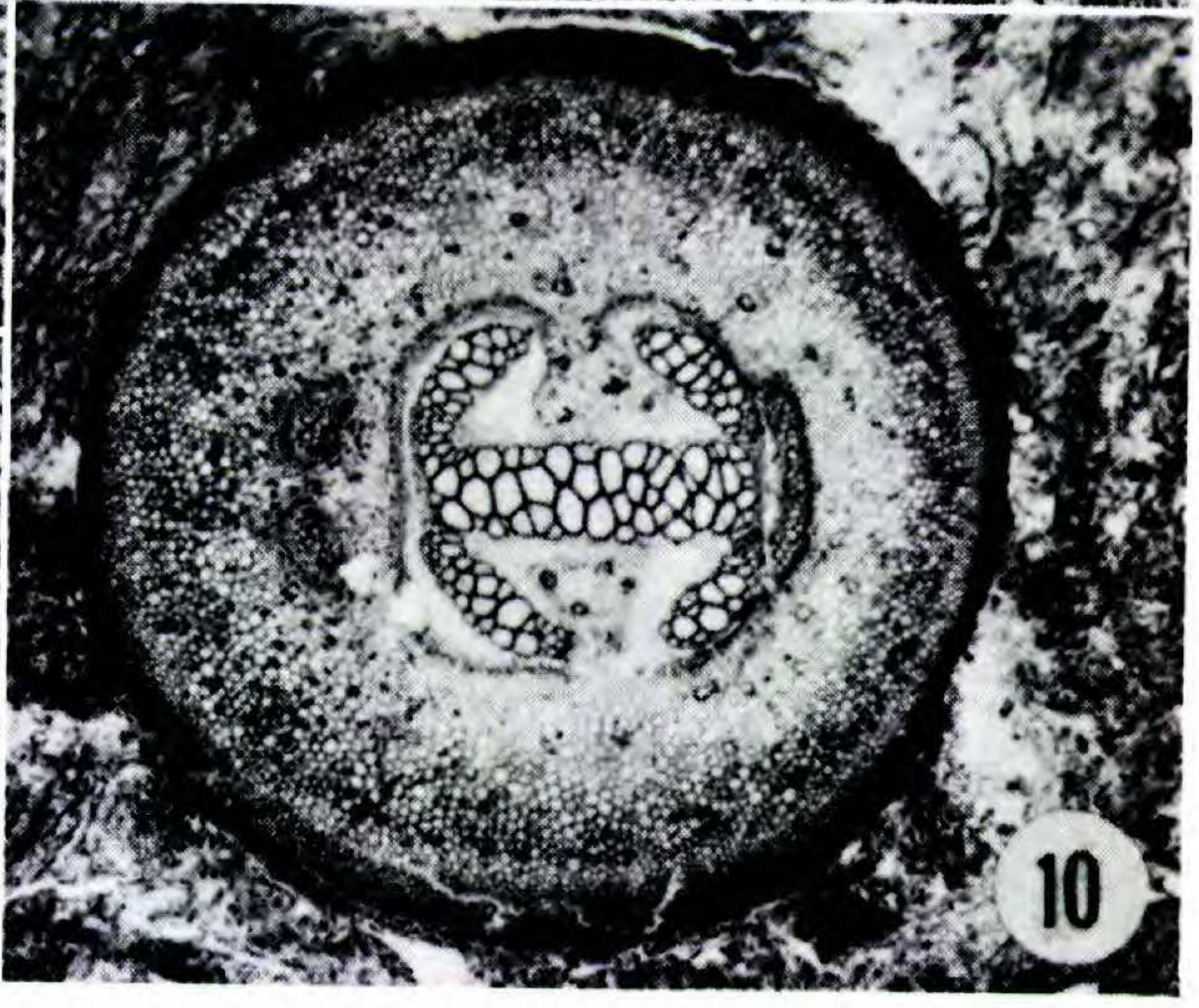
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but fertile pinna anatomy in *Biscalitheca* (Phillips & Andrews, 1968), *Notoschizaea* (*Alloiopteris*) (Fig. 21) and compression foliage of *Nemejcopteris* indicate that pinnate, biseriate divisions occurred in the more distal portions of etapteroid fronds and laminate pinnules were present in Pennsylvanian and Permian age representatives (Barthel, 1968; Nemejc, 1936).

CLEPSYDROIDEAE

The supposed evolutionary relationship between the late Devonian and early Mississippian *Clepsydropsis* forms and the Etapteroideae has been "primitive" and "derived" with considerable speculation regarding evolutionary changes of phyllophores and pinna emission (Sahni, 1918; Leclercq, 1931). In a more recent study of *Clepsydropsis* Galtier (1966*b*) has summarized anatomical details of eleven species, most of which have closed pinna traces and are typically biseriate. A newly described species, *C. leclercqii* from the lower Visean of France, may be regarded as an intermediate or transitional form between the Clepsydroideae and Etapteroideae with clepsydroid xylem, permanent peripheral loops, crescent-shaped pinna traces, and quadriseriate with quite a long undivided pinna trace below the dichotomy to a pinna-pair. The clepsydroid phyllophore xylem strand is 8 × 2 mm long with scalariform metaxylem and a massive pinna trace which extends more than 5 cm prior to division into a pair of shallow C-shaped xylem strands. *Rhacophyton* (Fig. 1D) has been considered to have another intermediate type of phyllophore anatomy between clepsydroid and etapteroid type fronds (Leclercq, 1951, 1954; Andrews & Phillips, 1968), with clepsydroid phyllophore vascular strands, secondary xylem, an opening in the peripheral loop with pinna emission, and both biseriate sterile and quadriseriate fertile pinnae. The pinnae derived from the phyllophore of zygopterid ferns exhibit xylary anatomy different from that of the phyllophore, but in *Rhacophyton* the clepsydroid phyllophore anatomy is repeated in the pinnae. It is interesting to note that such speculative evolutionary intermediates as *Rhacophyton* have secondary xylem present in the presumed phyllophores. *Clepsydropsis* is an organ genus of foliar members without stems, but the petioles of *Asterochlaenopsis* and *Austroclepsis* were assigned to *Clepsydropsis* by Sahni at one time.

ETAPTEROIDEAE

Within the Etapteroideae are both small and massive phyllophores (Figs. 1A–C, E–G) and some of the largest coenopterid ferns. *Metadineuron* and

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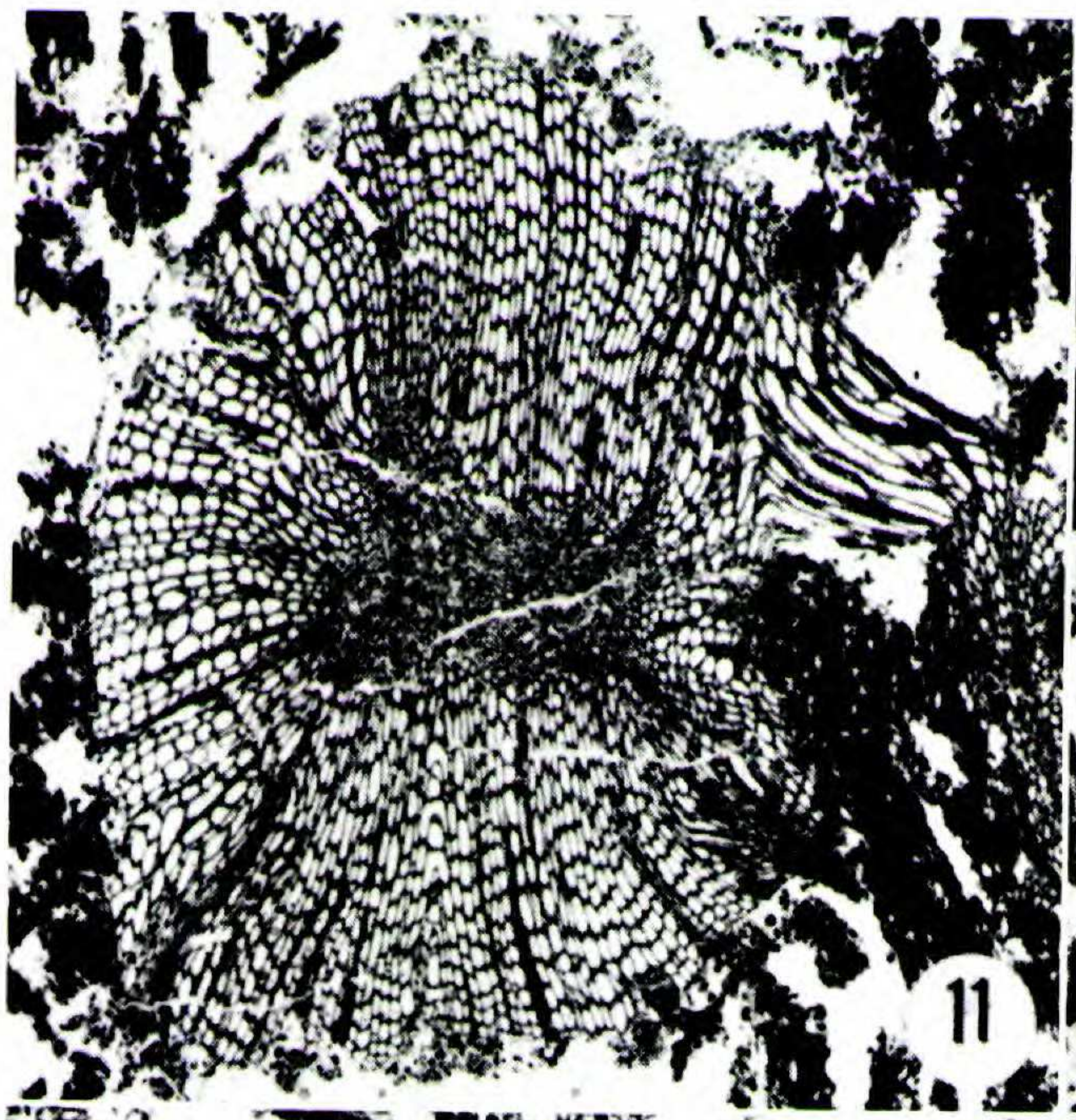
FIGURES 2–10.—2. *Metadineuron ellipticum*, x.s. phyllophore. Visean, Scotland. Kidston Coll. Hunterian Museum, Glasgow. × 20 (from Galtier, 1970).—3. *Dineuron pteroides*, x.s phyllophore. Visean, France. Montpellier Coll. × 20. (from Galtier, 1970).—4. *Botryopteris antiqua*, x.s. foliar member. Visean, France, Montpellier Coll. × 15 (from Galtier, 1970).—5–6. *Metaclepsydropsis duplex*, x.s. phyllophore and pinnae traces. Visean, Scotland. × 10.—7–8. *Diplolabis roemeri*, x.s. phyllophore and pinna trace. Visean, Scotland. × 10.—9. *Etapteris scotti*, x.s. phyllophore and pinnae traces. Mineral Coal, Kansas. × 10.—10. *Etapteris* sp., x.s. phyllophore and pinnae traces. Calhoun Coal, Illinois. × 10.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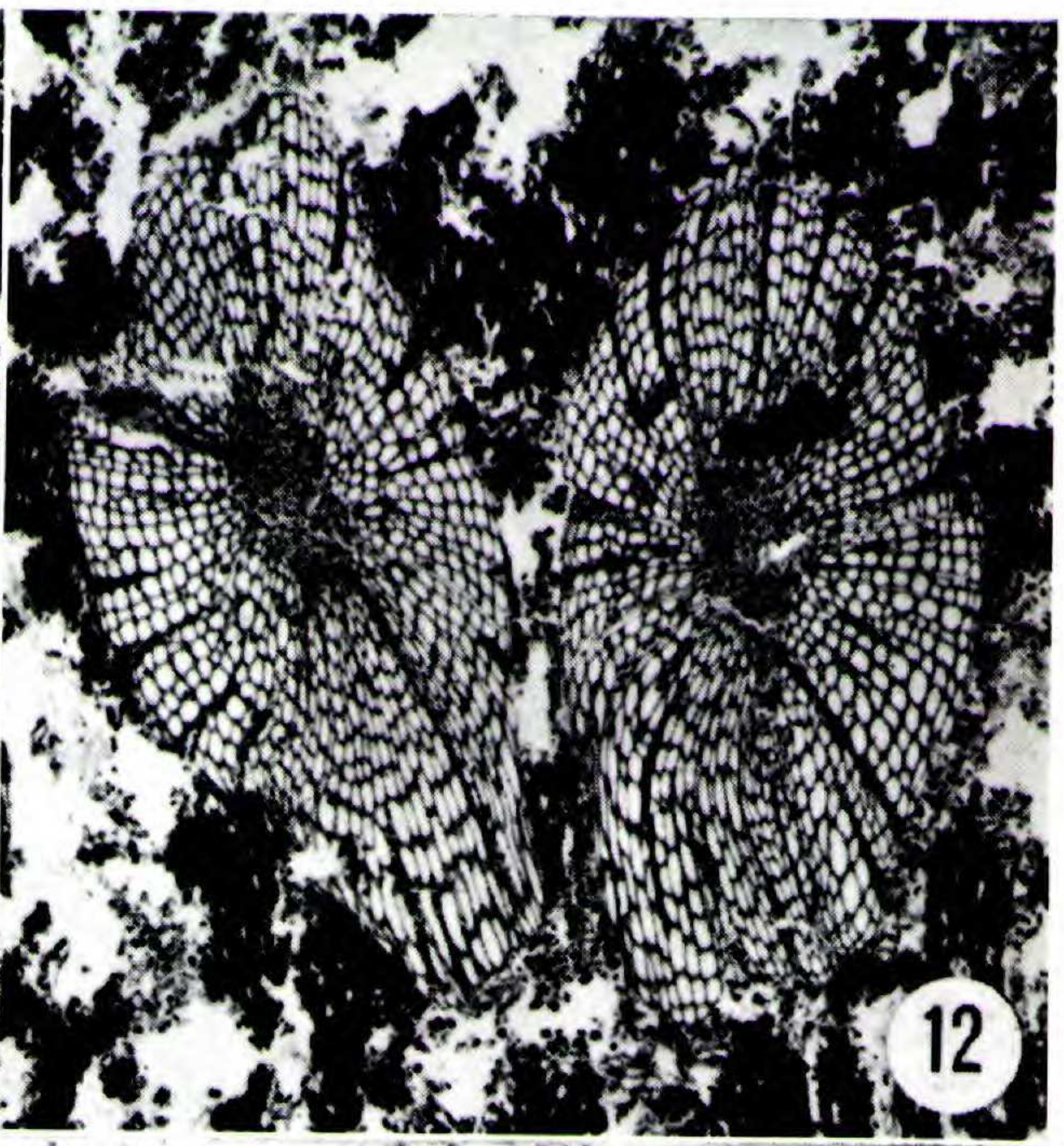
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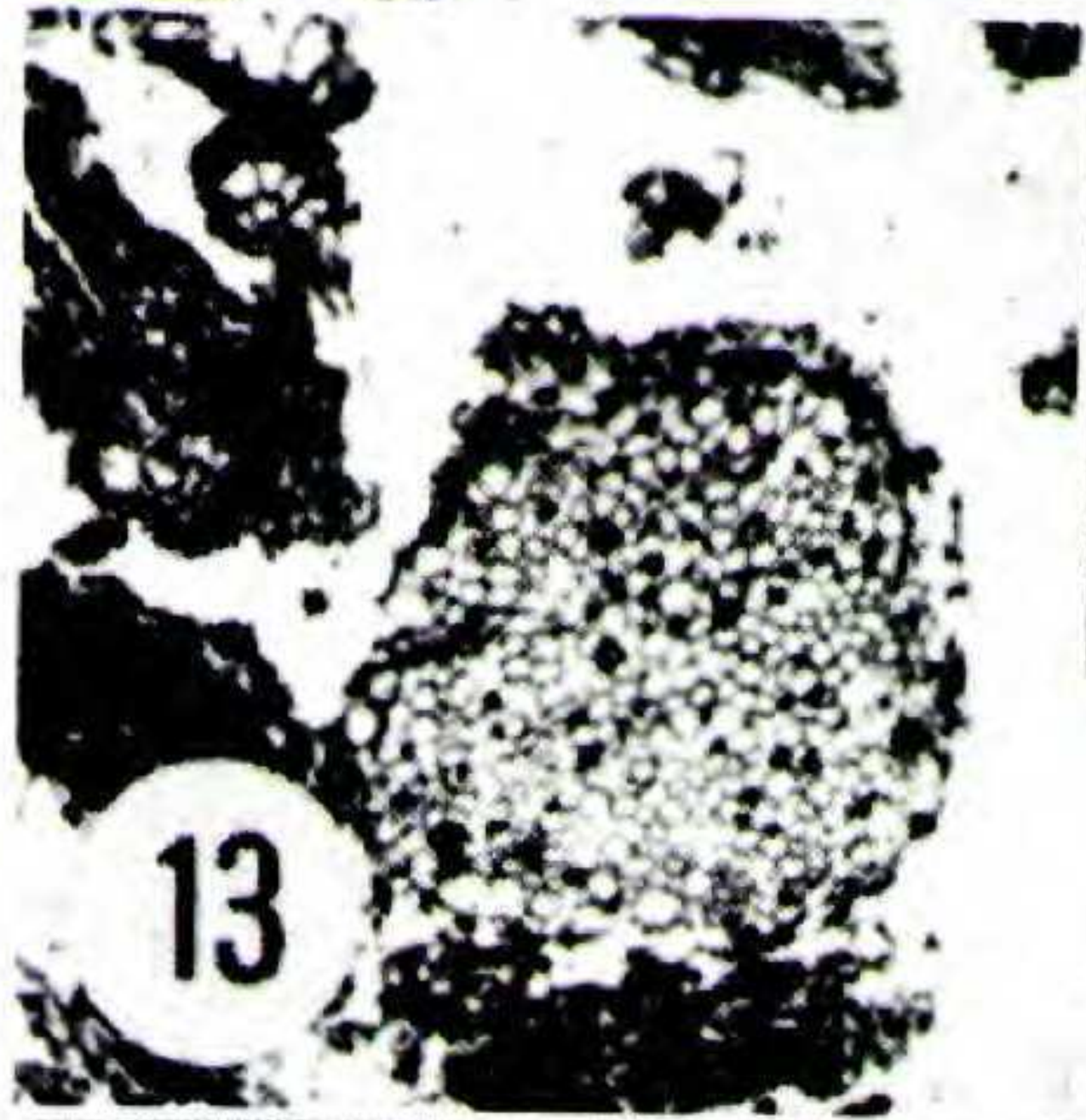
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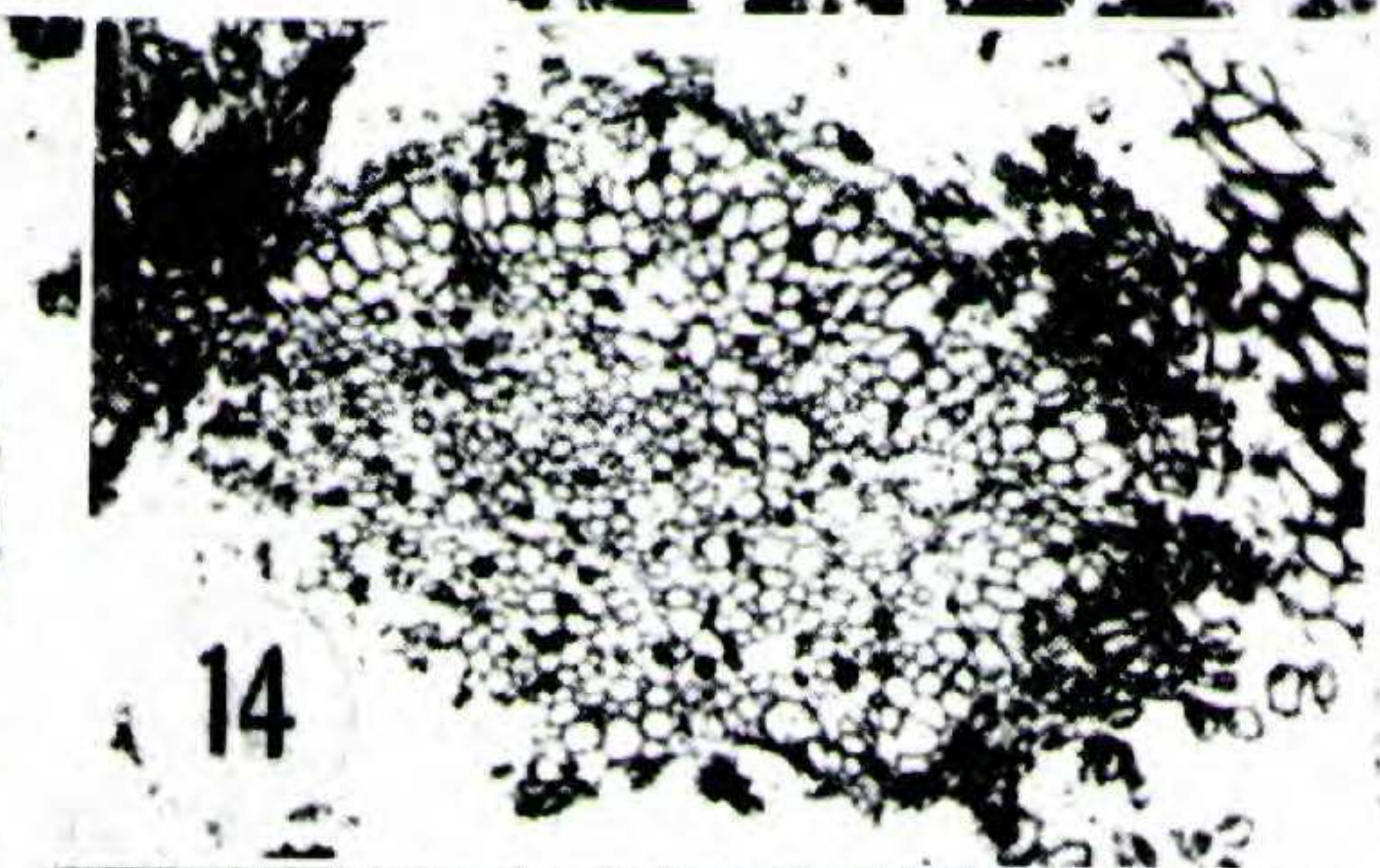
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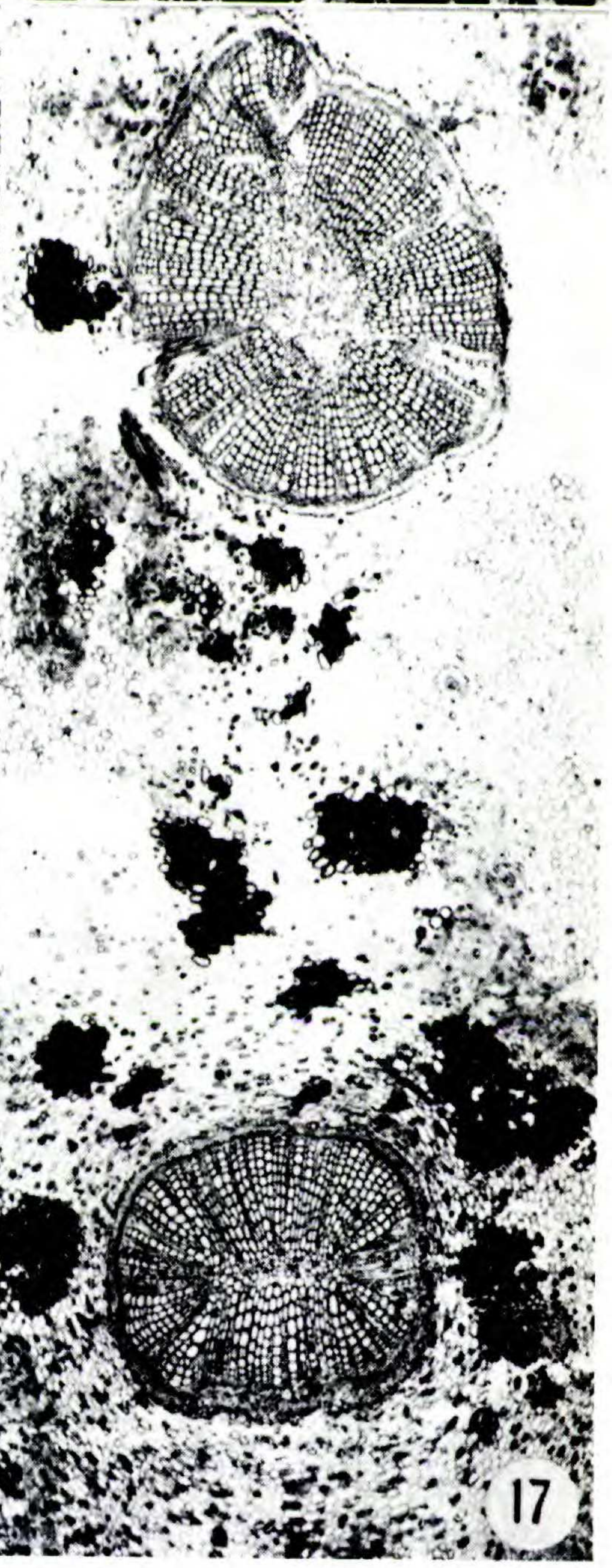
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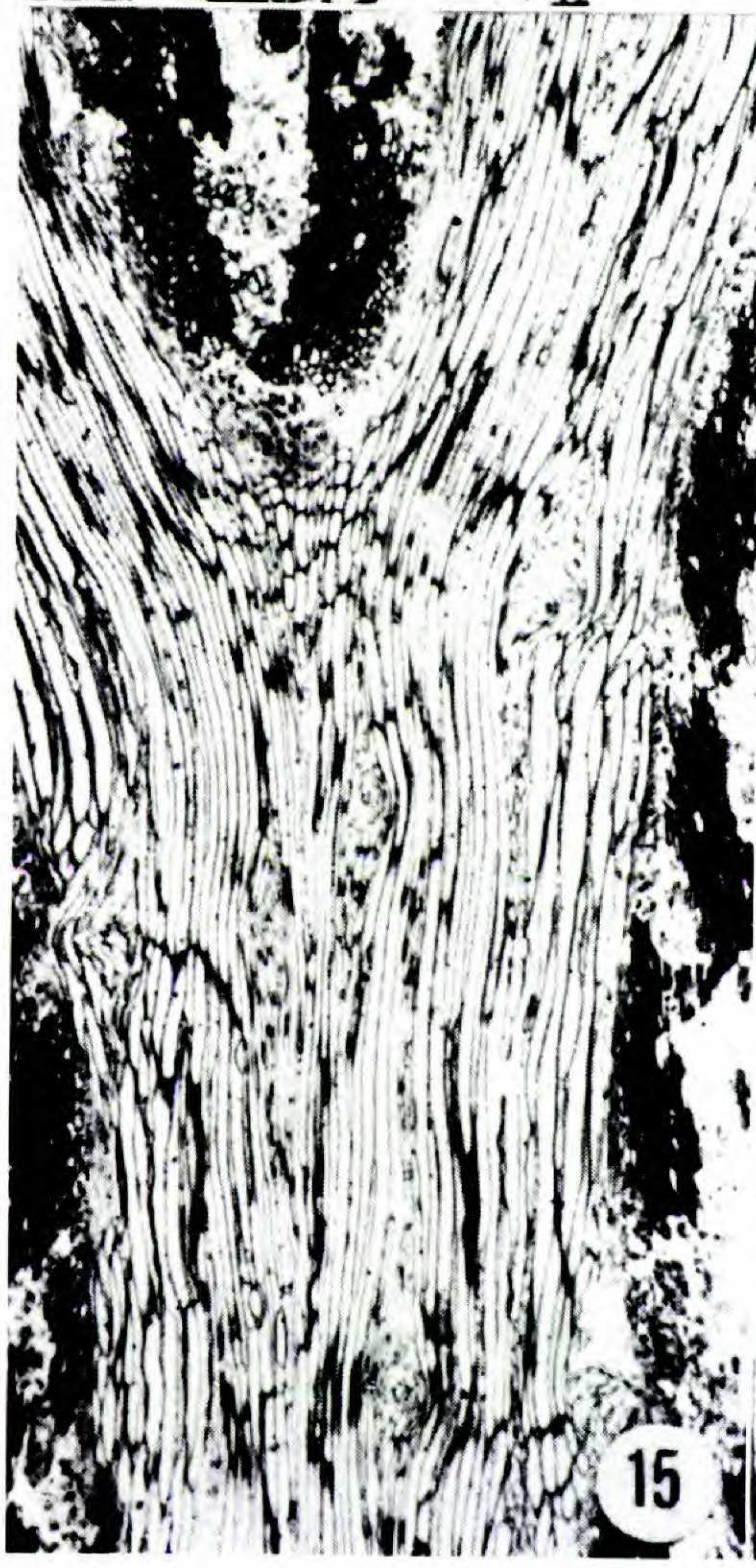
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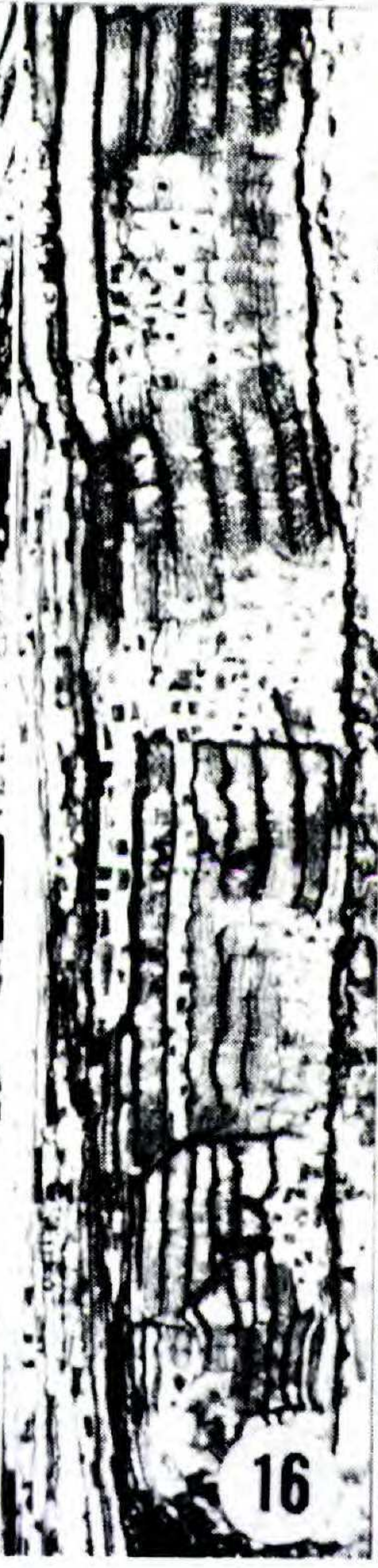
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Dineuron (Figs. 1A–C) are smaller phyllophore types with ellipsoidal xylem strands and with no known stems. *Metadineuron* (based on *Dineuron ellipticum* of Kidston, 1908) conforms to the pattern of pinna emission in *Metaclepsydropsis*, although dichotomy of the pinna trace into two pinna supplies has not yet been demonstrated (Galtier, 1964). *Dineuron*, which was previously thought to compare well with etapteroid types of phyllophores, exhibits a somewhat different kind of pinna emission than previously supposed. Within *D. pteroides* are two types of pinna emission which could be from the same frond (Figs. 1B, C). In one, the peripheral loops open, then close and reopen with separate C-shaped pinna traces departing from each margin of the opened loop; in the second type, a pair of small peripheral loops individually emit C-shaped pinna traces. The pinna traces are quite small compared to the phyllophore axis. The additional feature in pinna trace formation and emission of *Metadineuron* and *Dineuron* (Fig. 1B) shared with other etapteroid genera is the common trace stage or temporary union of xylem of the pinna-pair (Figs. 1E–G, 5–10).

Zygopteris primaria from the Permian had an erect habit with branching unknown (Sahni, 1932*a*); other species of *Zygopteris* are rhizomatous and dichotomously branched (Figs. 12, 15) with distantly spaced leaves in two lateral rows. *Metaclepsydropsis, Diplolabis, Ankyropteris corrugata*, and *Nemejcopteris* also have rhizomatous habits with dichotomous branching. Aphlebiae occur on the rhizomes and lower part of the petioles in *Zygopteris* and *Ankyropteris*, and all around the base of the frond and at bases of quadriseriate pinnae in *Nemejcopteris* (see Holden, 1930; Baxter, 1951).

Anatomically one of the unusual features of *Zygopteris* is the presence of secondary xylem (Scott, 1912*a*; Holden, 1955; Andrews, 1942), an interpretation which has been questioned by Baxter (1952) on pertinent points. In a study of American *Zygopteris* stems Dennis (1972) has presented quite convincing evidence of the secondary origin of the outer xylem. Primary xylem near the apex lacks radial files of larger tracheids (Figs. 13–14), there is a basipetal increase in the number of tracheids in radial files, and uniseriate rays are demonstrable in both tangential (Fig. 15) and radial section (Fig. 16). The lateral meristem that produced secondary xylem in *Zygopteris* was apparently active in younger regions of the stem and did not persist.

Among the anatomically better known zygopterid genera are *Metaclepsydropsis, Diplolabis*, and particularly *Zygopteris*. The protostelic anatomy of these genera may be compared along with that of *Ankyropteris corrugata*. Each has a stellate central core of xylem with peripheral protoxylem groups and is surrounded by larger tracheids showing at least some degree of radial alignment. *Diplolabis* from the Visean of Scotland has a solid protostele composed

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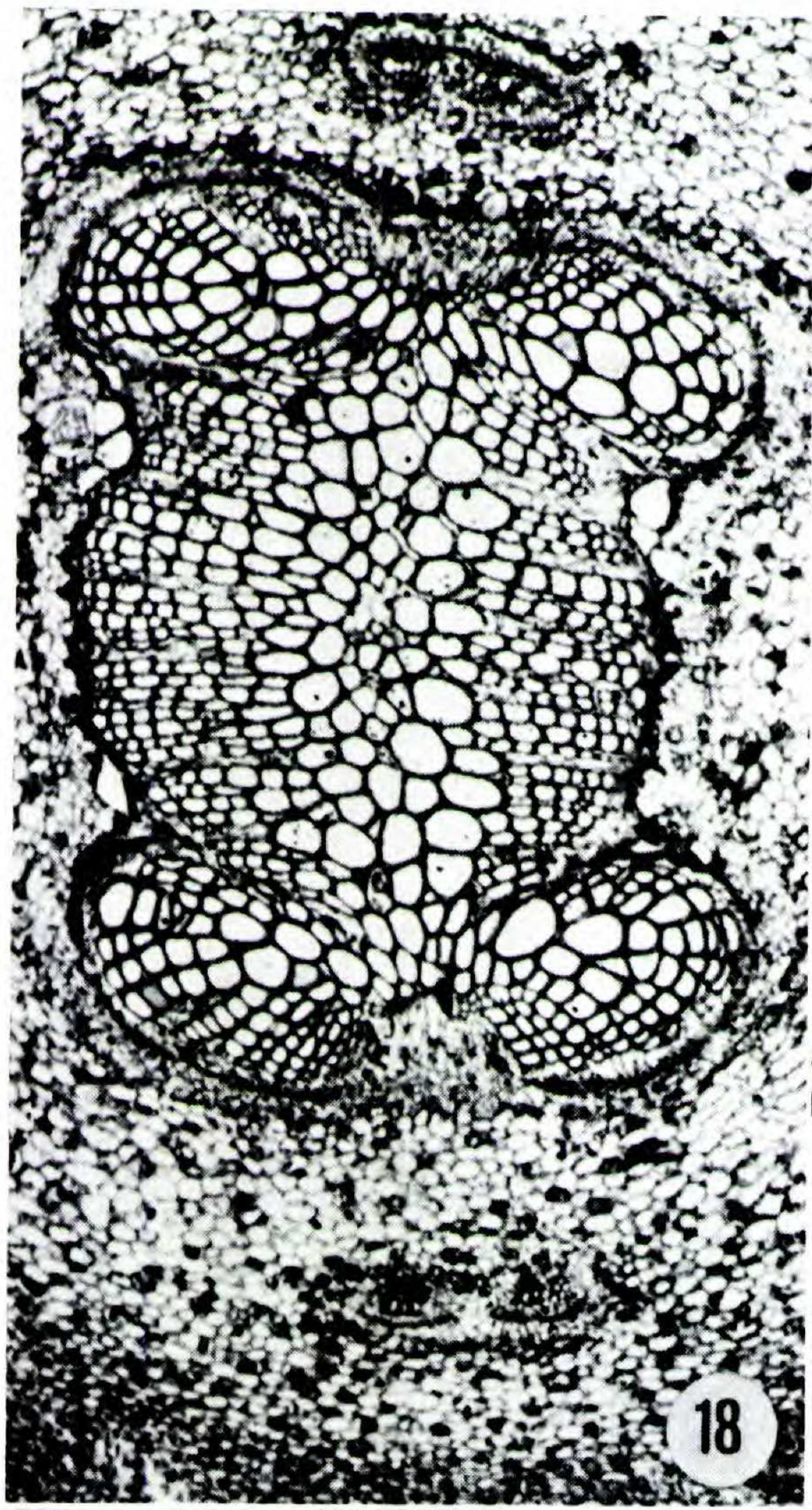
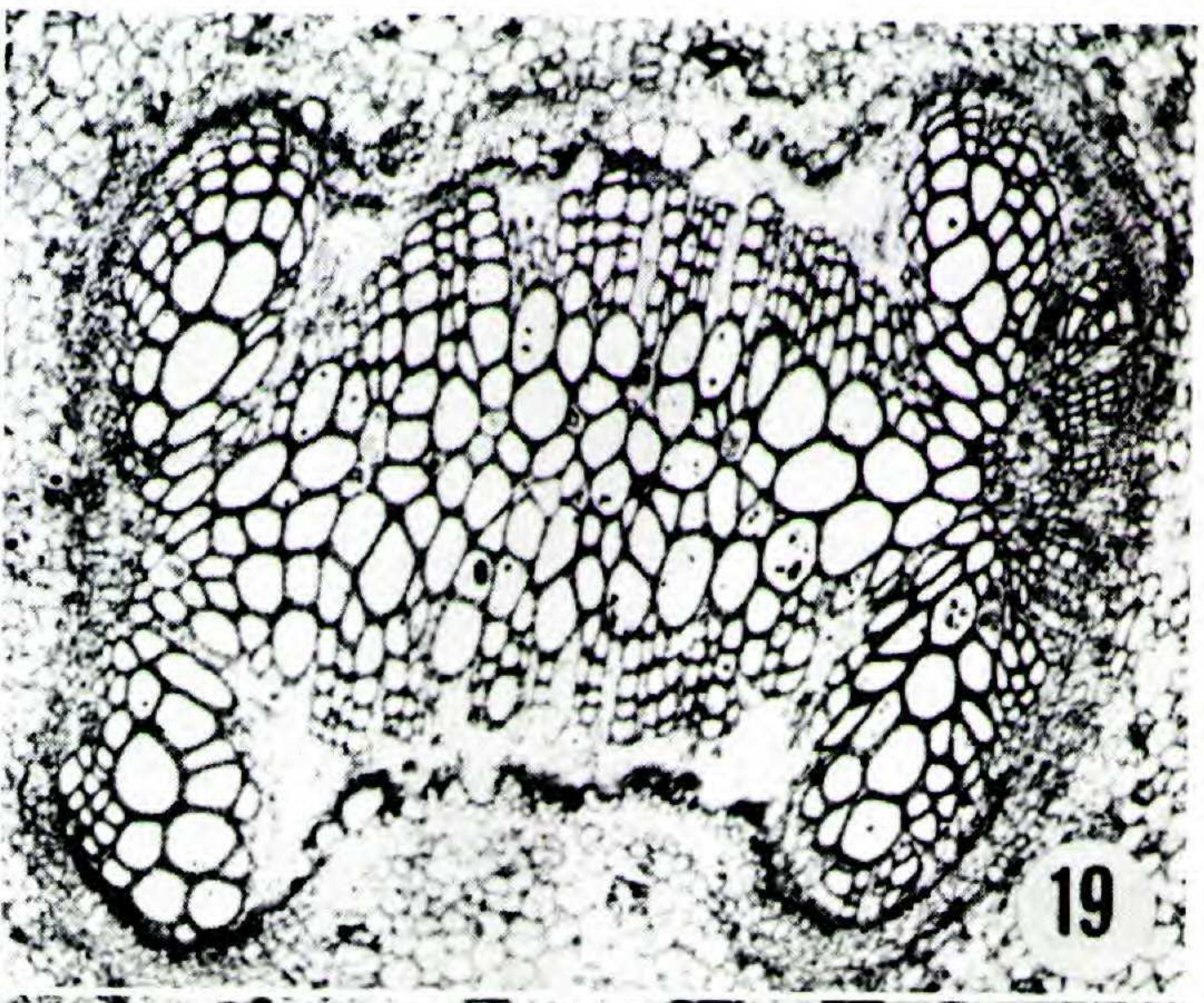
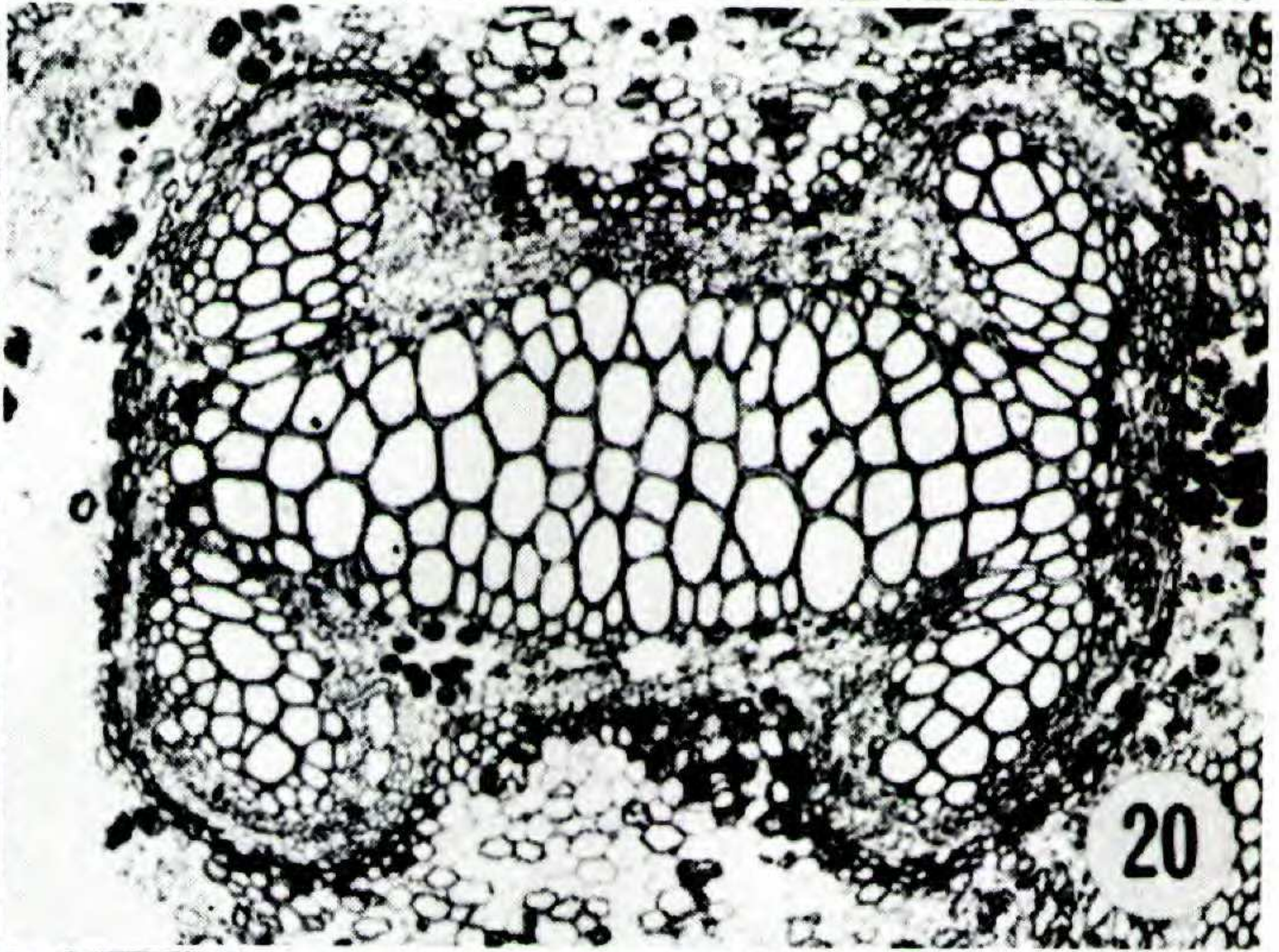
FIGURES 11–17. *Zygopteris* anatomy.—11–12. *Z. illinoiensis*, x.s. xylem of rhizome below and above dichotomy. Herrin Coal, Illinois. × 10.—13–14. *Zygopteris* sp. x.s. primary xylem near apex of rhizome. Calhoun Coal, Illinois. × 25.—15–16. *Zygopteris* sp. tangential and radial sections of secondary xylem of rhizome showing rays. Calhoun Coal, Illinois. × 10, × 25.—17. *Zygopteris* sp. x.s. rhizome and phyllophore trace (below) with secondary xylem. Calhoun Coal, Illinois. × 10 (figures 13–17 from Dennis, 1972).







FIGURES 18–20. *Zygopteris* sp. phyllophore trace at higher levels with diminishing amount of secondary xylem. Calhoun Coal, Illinois. × 25 (from Dennis, 1972).—21. *Notoschizaea robusta*, x.s. pinnules. "Baker" Coal, Kentucky. × 25.

of an inner zone of shorter- and smaller-diameter tracheids (Gordon, 1911*a*). Of the same age, *Metaclepsydropsis* indicates that the mixed protostele occurred early in zygopterid evolution (Gordon, 1911*b*); the inner primary xylem of the rhizome consists of tracheids and parenchyma as it does in the lower Westphalian A species *Ankyropteris corrugata* (Holden, 1930) and Pennsylvanian species of *Zygopteris* (Scott, 1912*a*; Andrews, 1942; Baxter, 1952; Dennis, 1972). An increase in stelar parenchymatization in Middle and Upper Pennsylvanian species of *Zygopteris* is suggested by Dennis (1972).

Petiolar trace formation and emission in these taxa is quite similar. There is an oval bipolar (two protoxylem groups) trace which originates in the outer xylem of *Diplolabis* and *Metaclepsydropsis*, from both inner and outer xylem in *A. corrugata*, and from strictly the inner (primary) xylem in *Zygopteris*. Traces take on an elongate bar-shaped configuration; protoxylem groups divide to form a tetrapolar petiolar strand; peripheral loops appear, and in *Zygopteris* antennae develop. Along the course of the petiolar trace in *Zygopteris* there may be a variable amount of secondary xylem (Fig. 17) which diminishes upwardly and the antennae become distinct (Figs. 18–20); aphlebia-pair traces are emitted at this level (Fig. 18). More prominent antennae develop at higher levels, and pinna trace emission begins (Figs. 9–10).

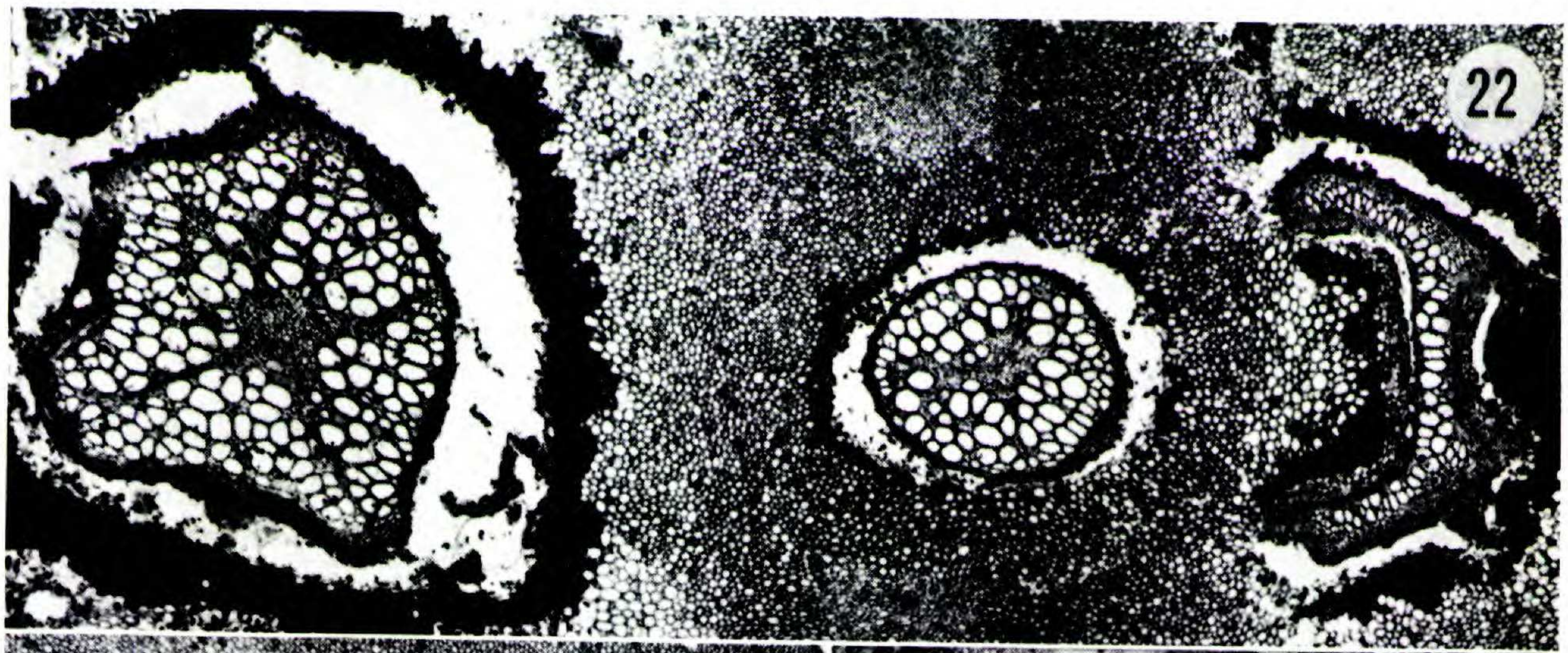
The best known zygopterid assemblage from compression studies is *Nemejcopteris (Pecopteris) feminaeformis*, a *Zygopteris*-like plant known from the Lower Permian of East Germany (Barthel, 1968). The creeping dichotomous rhizome was up to 6 mm in diameter and densely pilose with spine-like hairs up to 3 mm long. Quadriseriate phyllophores were erect upon the rhizome. Evidence of roots was lacking. The phyllophore also had long stiff hairs and attained diameters up to 7 mm with preserved lengths of 40 cm; the tip of the phyllophore exhibited circinate vernation. At the base of each pinna pair are aphlebiae. Pinnae are once pinnately branched and bear laminate pinnules of the *Pecopteris* type. Sterile foliage similar to that of *Nemejcopteris* is widely distributed in the Stephanian and Lower Permian (Barthel, 1968).

ANKYROPTERIS

The genus *Ankyropteris* includes two groups of species; those known only from foliar members and those with both stems and petioles. The earliest occurrences of isolated foliar members are in the Upper Mississippian of Arkansas (Taylor & Eggert, 1967) and the Namurian of Poland (Corsin, 1952), and the isolated foliar members have been compared in detail by Baxter (1951) and Corsin (1952). The earliest stratigraphic records of species with known stems and petioles are all Lower Pennsylvanian (*A. hendricksii*, *A. grayi*, *A. corrugata*). *Ankyropteris glabra* from the Middle and Upper Pennsylvanian of the U.S.A. is one of the most completely known Paleozoic ferns and differs slightly from *A. grayi* (lower Westphalian A of England) which has shorter internodes and more mixed parenchyma and tracheids in the center of the stem. *Ankyropteris scandens* from the Lower Permian is apparently quite similar to *A. grayi*.

The earliest known shoots of *Ankyropteris* indicate three habits. *Ankyropteris hendricksii* (Read, 1938) from Oklahoma has very closely spaced petioles and densely packed ramentum and roots which give a "false stem" aspect to the erect habit. *Ankyropteris corrugata* exhibits a rhizomatous or climbing habit with dichotomous branching, unassociated with leaves. *Ankyropteris grayi* and *A. glabra* were probably upright climbing plants, and *A. glabra* is often found preserved alongside *Psaronius* stems and their root mantles.

The morphology of *A. glabra* is best known, and with the above mentioned differences may serve as an anatomical representative of the group, although comparable details of frond morphology are not known for other species (Baxter, 1951; Andrews, 1956; Eggert, 1959*a*, 1963; Eggert & Taylor, 1966). The stele is a pentarch actinostele with an inner network of mixed parenchyma and small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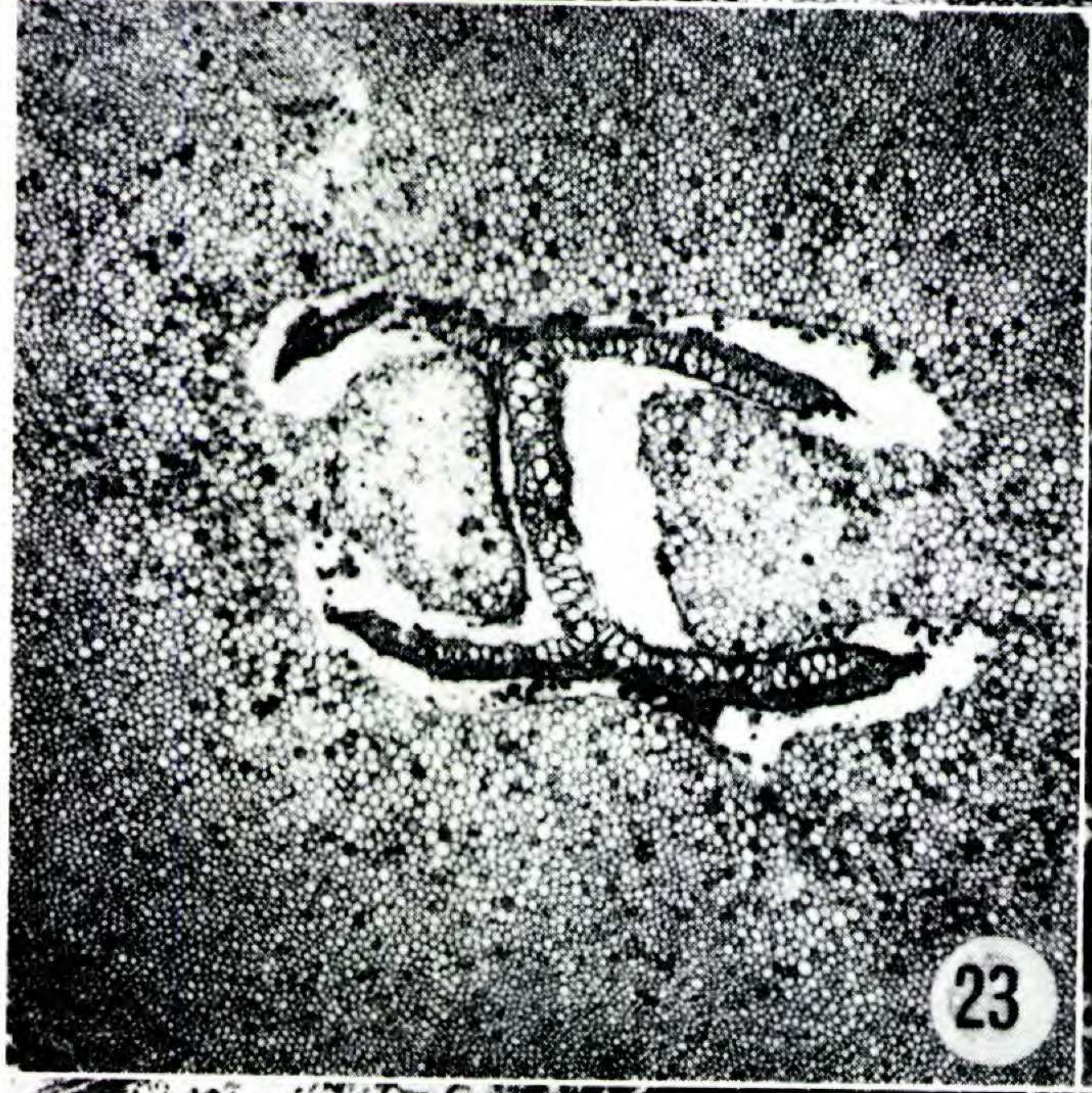
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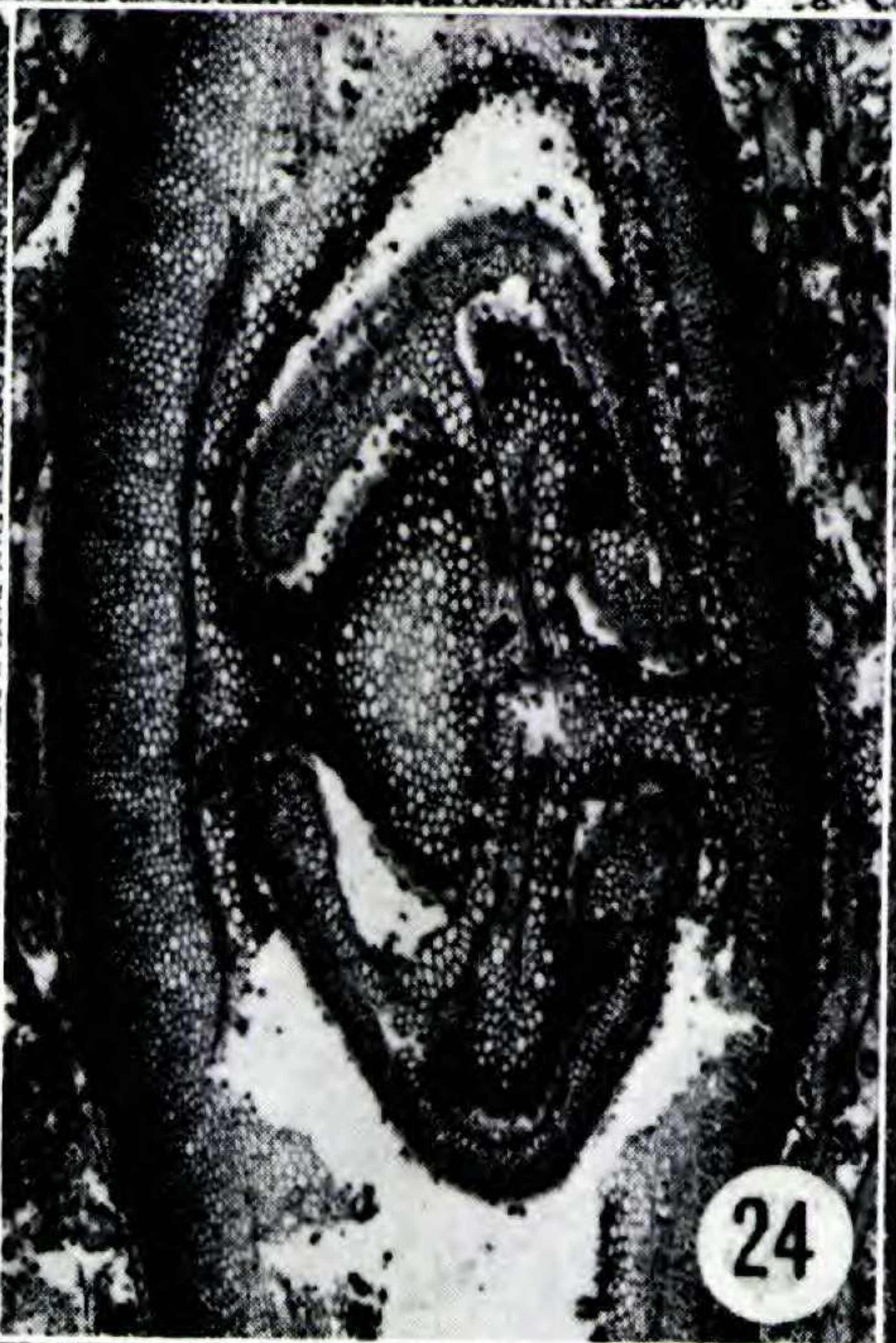
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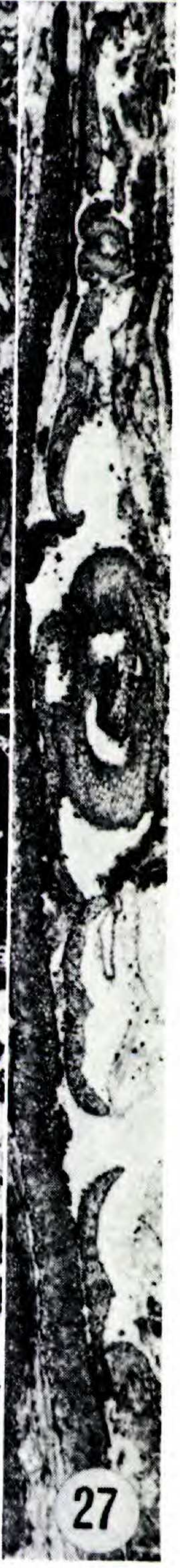
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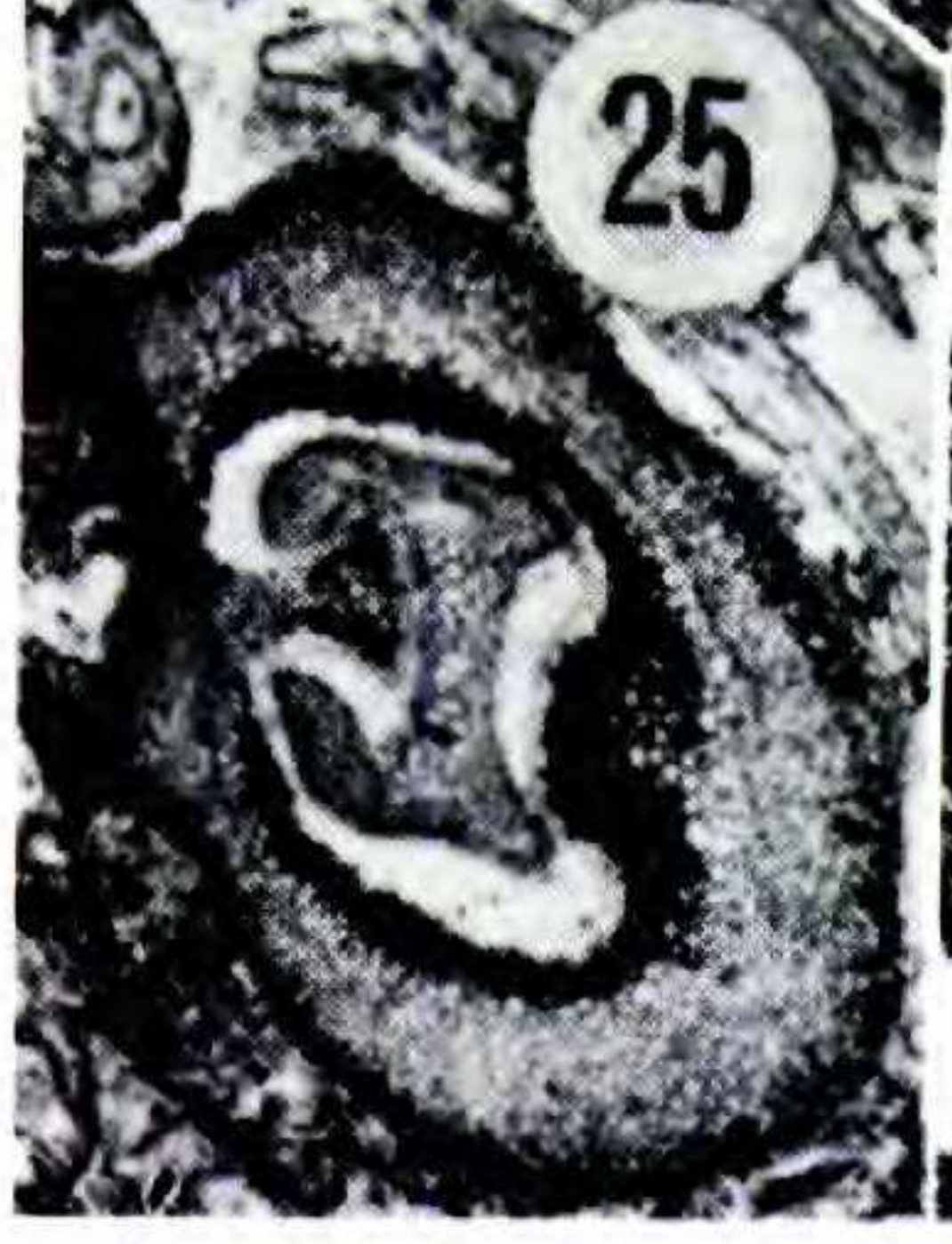
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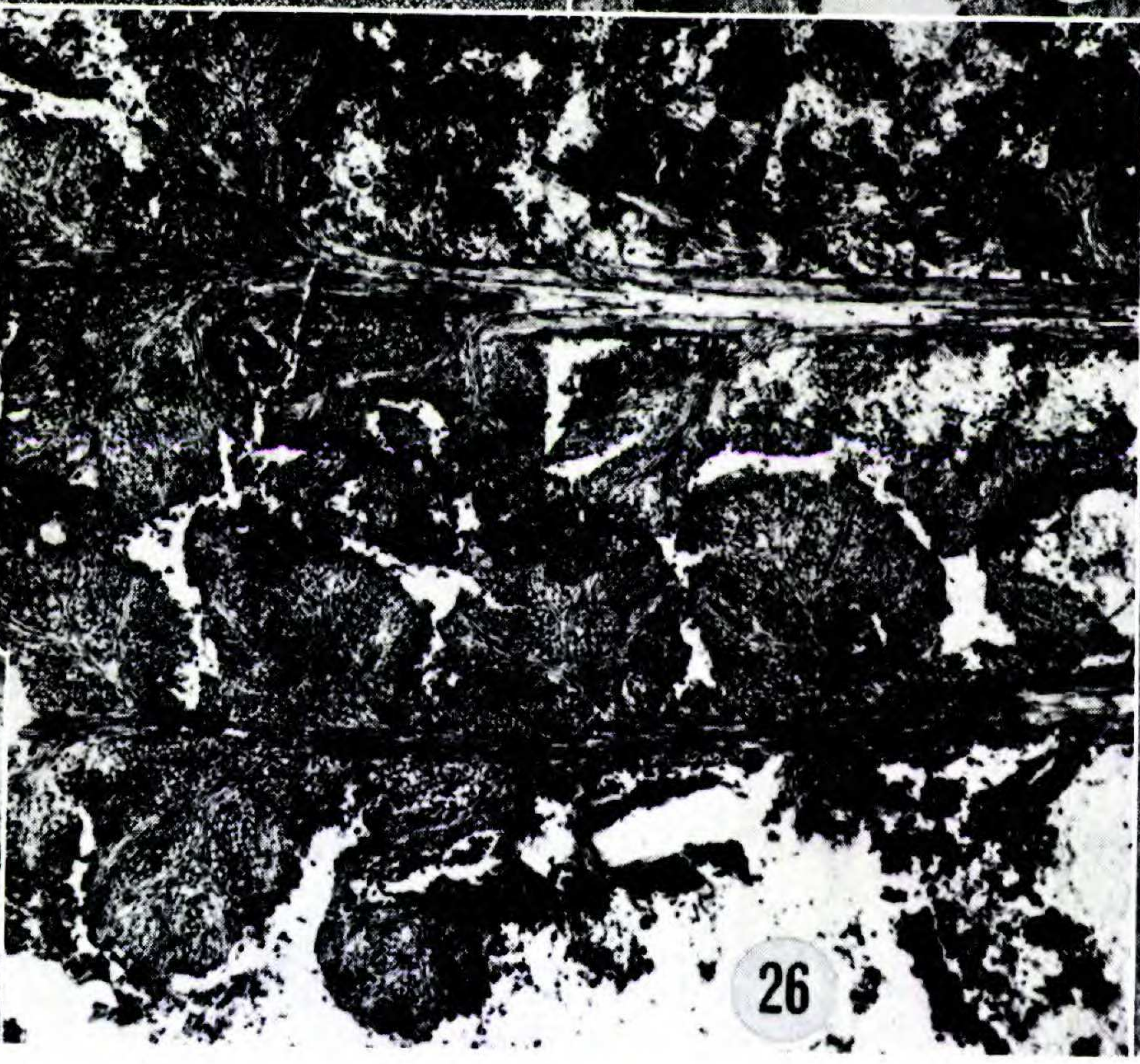
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diameter scalariform tracheids, surrounded by scalariform metaxylem elements (Fig. 22). Branching is axillary with either a common trace giving rise to the terete axillary stele and the di-upsilon phyllophore trace (Baxter, 1951) or with the branch stele arising from the stem above the point of petiole trace departure (Andrews, 1956). Development of axillary branches in *A. glabra* normally took place, resulting in several successive orders of stems and petioles which were progressively smaller and simpler in structure with determinate growth (Eggert, 1959*a*). The stem system and petiolar bases (see fig. 14 in Eggert, 1959*a*) are cloaked with numerous aphlebiae and multicellular uniseriate hairs. Despite the H-shaped zygopterid phyllophore and peripheral loops of *A. glabra* (Fig. 23) the frond was biseriate and quite similar to modern ferns in its pinnately compound, planated pinnae with small laminate pinnules of a *Pecopteris* type. The primary pinnae are supplied from the adaxial antennae and are slightly turned toward the stem; their xylem stages have adaxial antennae (Figs. 25, 27) and small abaxial lobes. These in turn bear secondary ultimate pinnae with terete xylem strands which bear the pinnules (Fig. 26). Basalmost pinnule-pairs are slightly larger and have a somewhat undulating margin like those shown by Eggert and Taylor (1966) in the fertile foliage. A scale-like aphlebia occurs on the adaxial side of the petiole at the base of each pirmary pinna (Eggert, 1963). The vascular configuration of the rachis of *Ankyropteris glabra* changes distally (Fig. 24); it resembles that of the European *A. westfaliensis* which, by parallel, may be the distal part of the rachis of *A. grayi* (Scott, 1912*b*; Eggert, 1963).

Ankyropteris glabra has been regarded as the first recognizable member of an extinct family which combines somewhat zygopterid anatomy (shared with *Ankyropteris* species, *Asterochlaena*, *Asterochlaenopsis* and *Austroclepsis*) with planated biseriate laminate fronds (Eggert & Taylor, 1966).

ANACHOROPTERIDACEAE

Among genera included in the Anachoropteridaceae with abaxial curvature of petiolar xylem strands are *Tubicaulis* (Figs. 37–42), *Anachoropteris* (Figs. 44–50), *Psalixochlaena* (Figs. 28–36), and *Apotropteris* (Figs. 54–55). *Tubicaulis* and *Anachoropteris* occur from lower Westphalian A to Permian; *Psalixochlaena* is known only from the lower Westphalian A of western Europe; and *Apotropteris* is known only from the Upper Pennsylvanian of the U.S.A.

Solid and mixed protosteles are exhibited by the genera, and siphonosteles are known from current studies. Stelar evolution within the Anachoropteridaceae has followed two general pathways with the retention of a solid protostele in one phyletic line of *Tubicaulis* as well as the Pennsylvanian species *Psalixochlaena cylindrica*, *Anachoropteris clavata*, and some stems of *Apotropteris minuta*.

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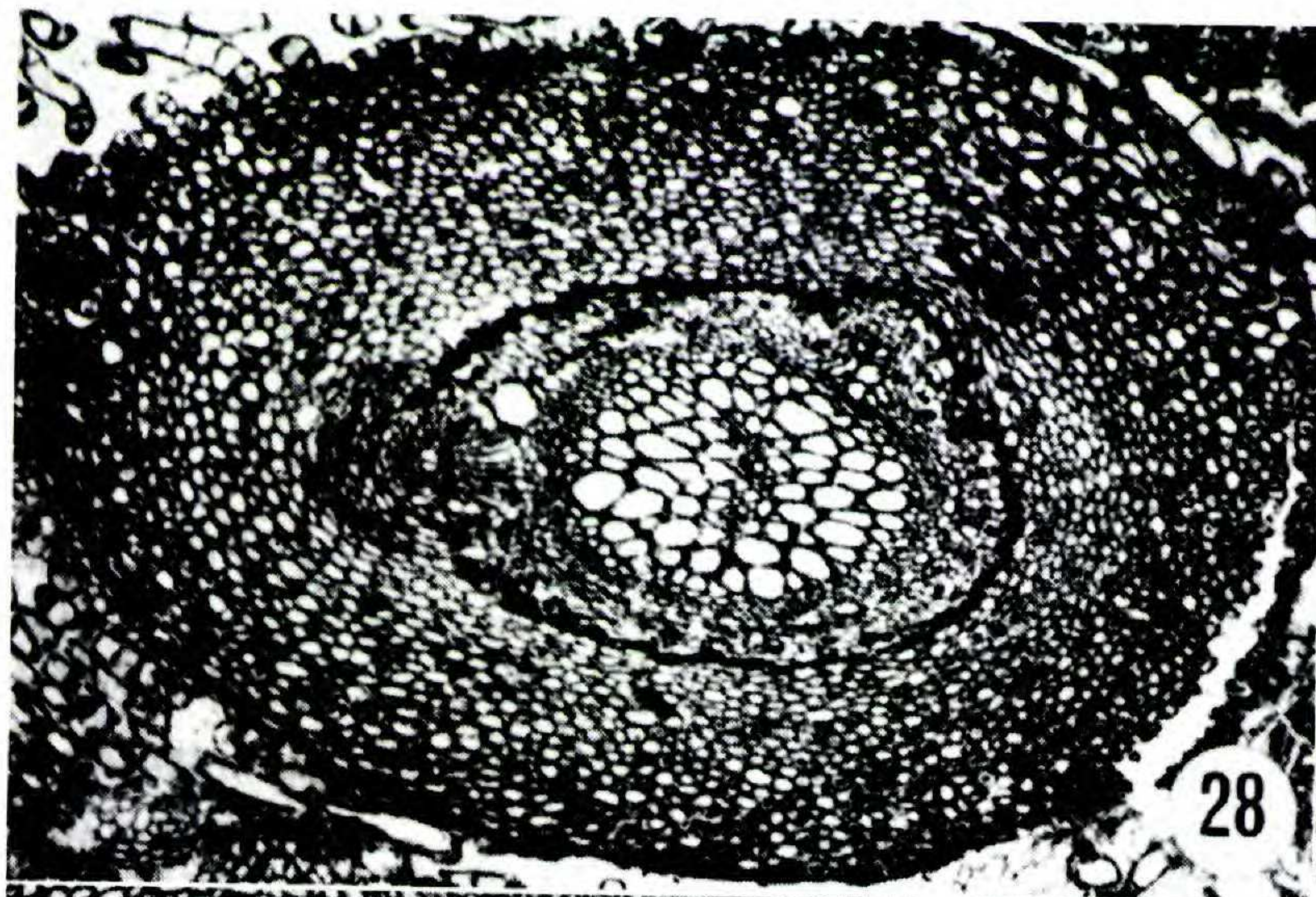
FIGURES 22–27. *Ankyropteris glabra* stem and frond anatomy. Herrin Coal, Illinois. × 10. Adaxial face of all foliar cross-sections is oriented to left except Fig. 23.—22. Stem and axillary branch steles with petiolar trace at right.—23. Petiole x.s.—24. Rachis x.s. distal.—25. Pinna x.s.—26. Pinnules in paradermal section.—27. Pinnae and laminate pinnules x.s.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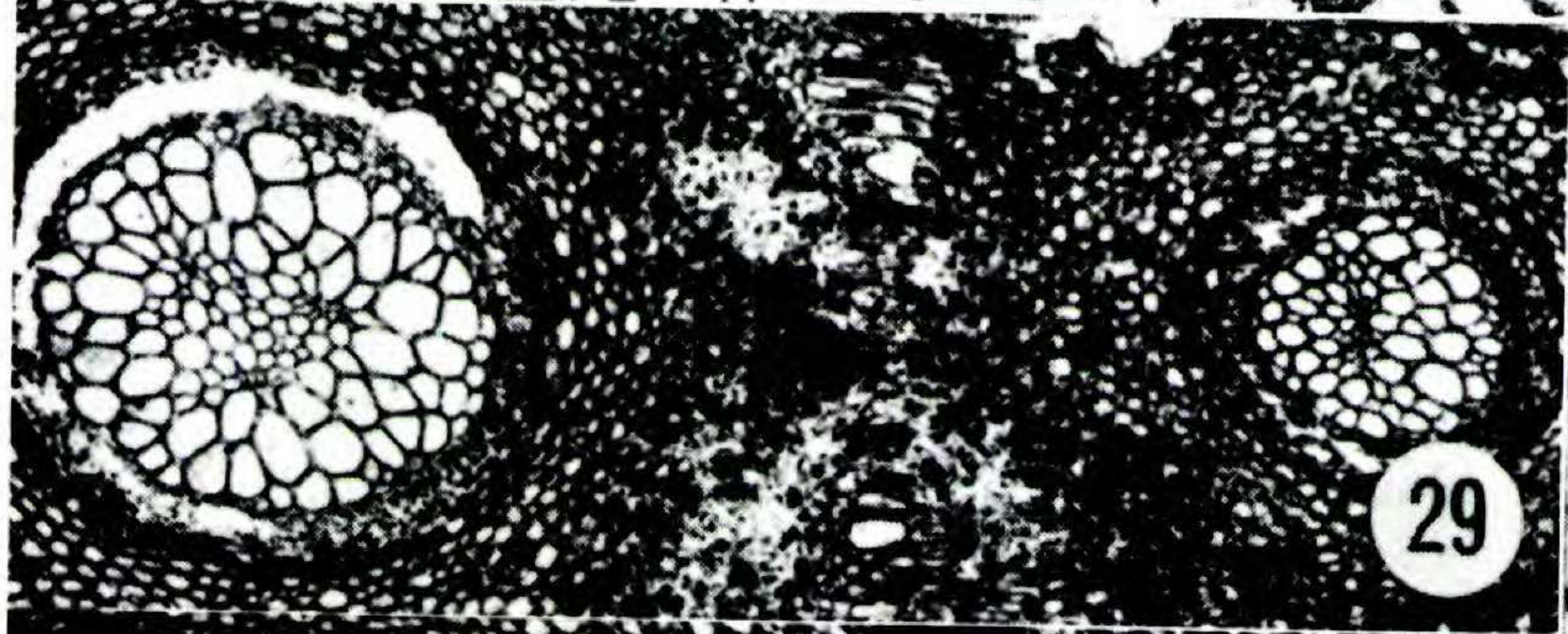
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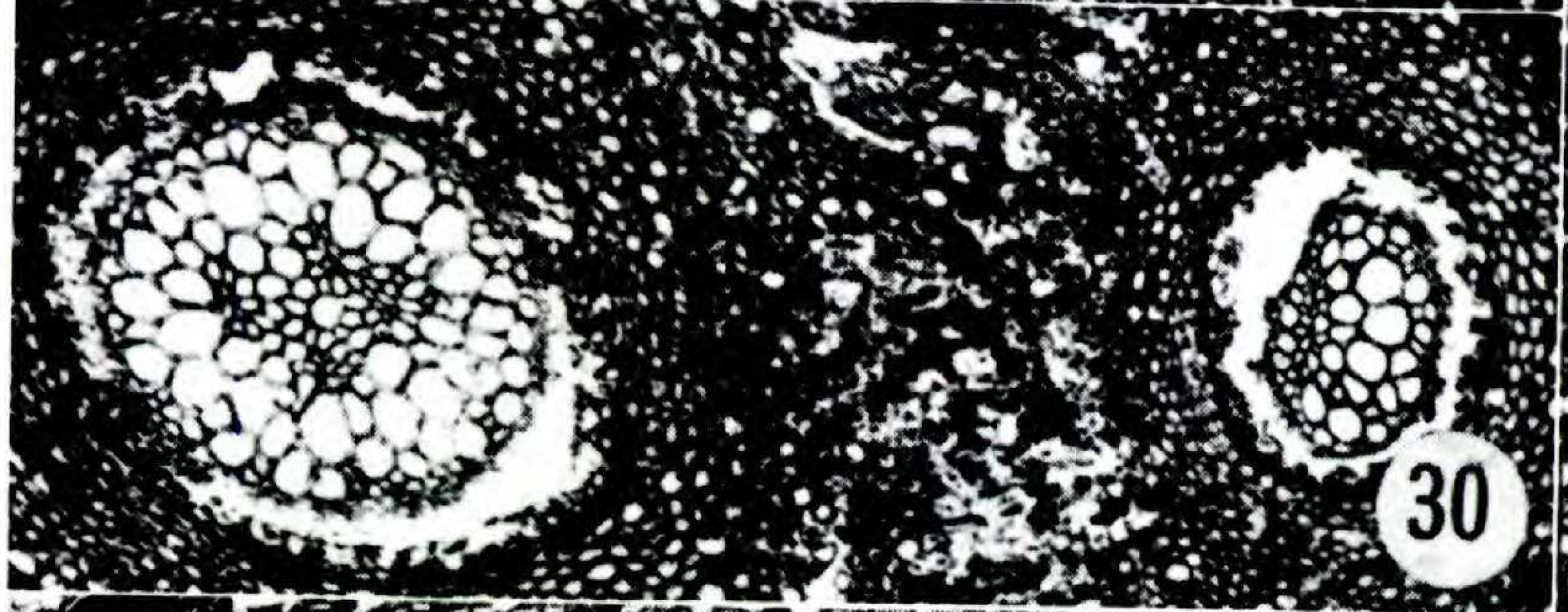
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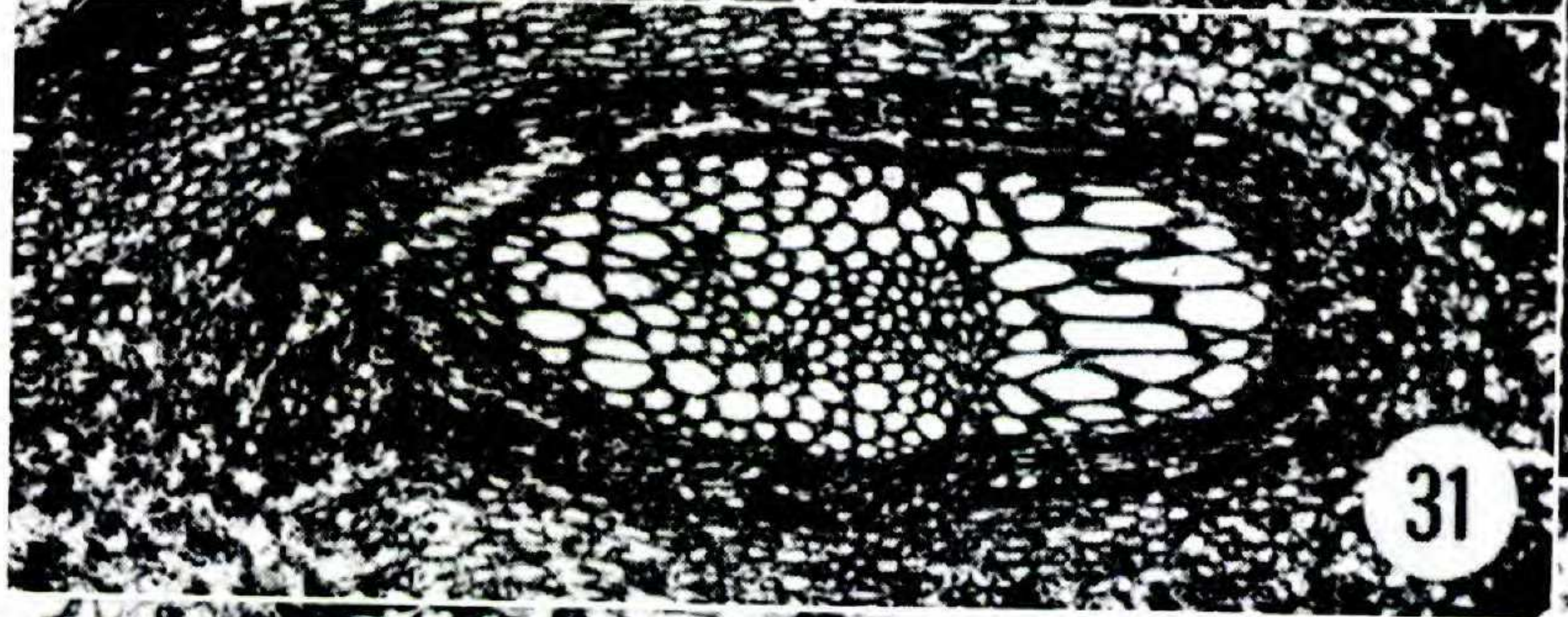
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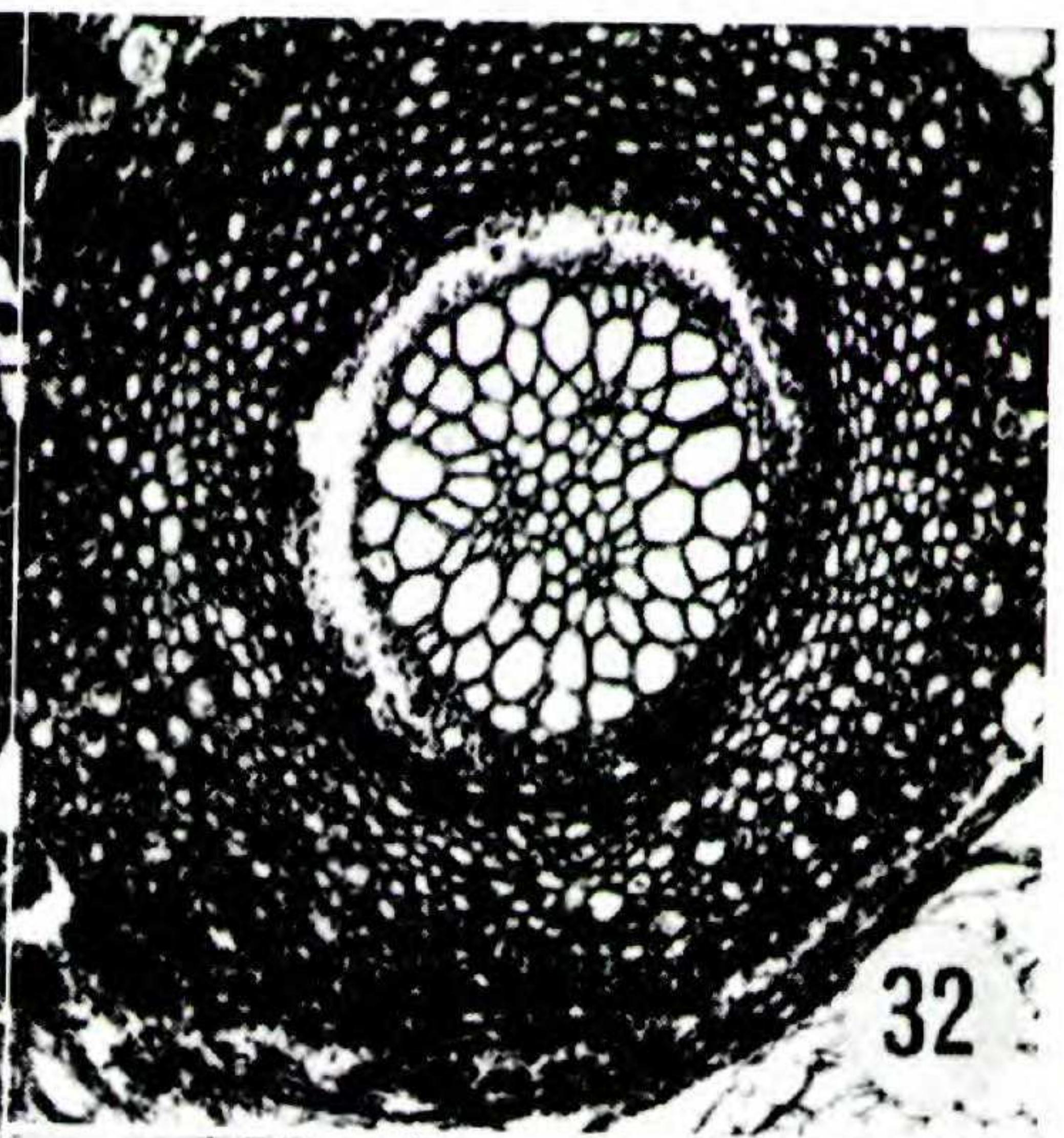
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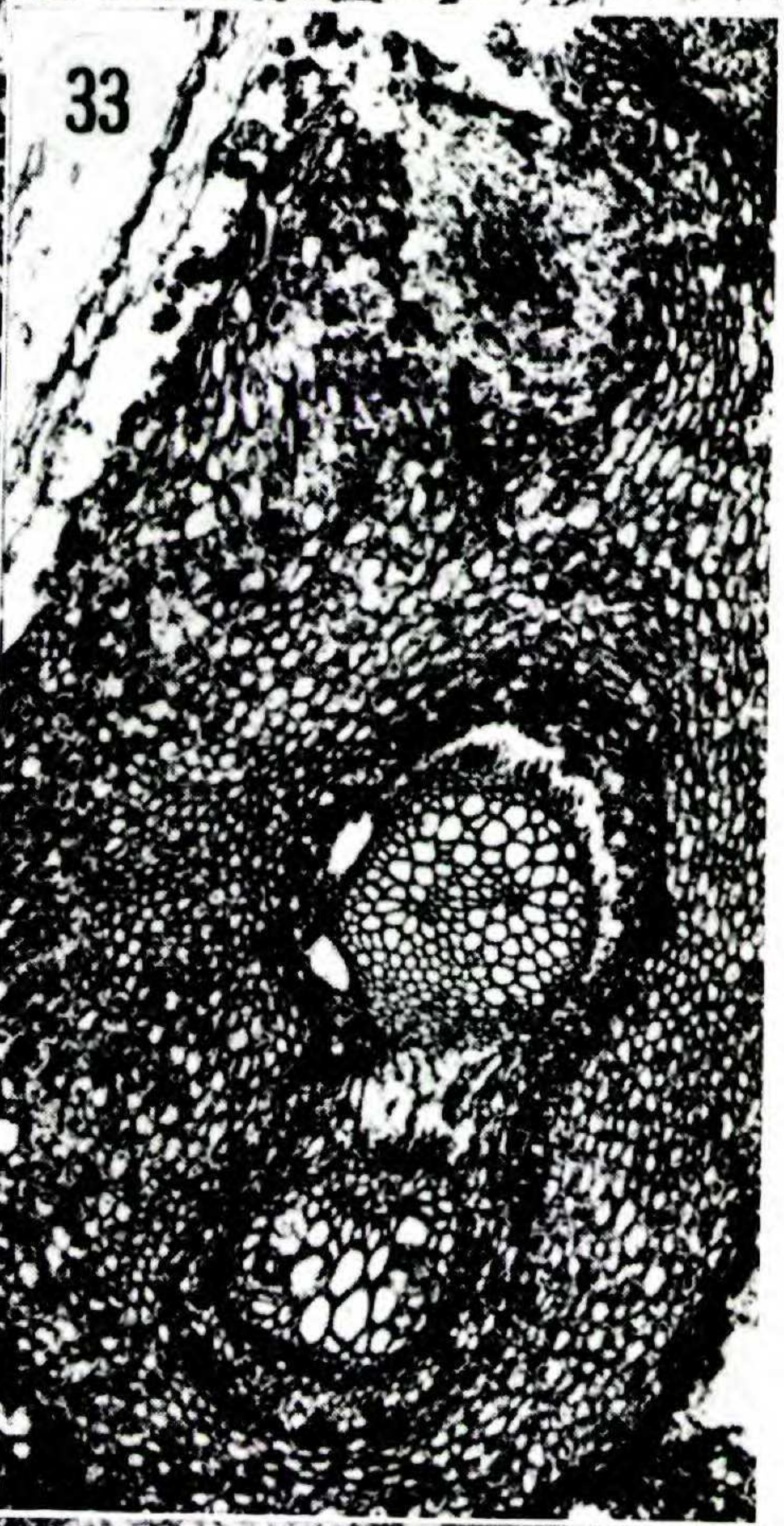
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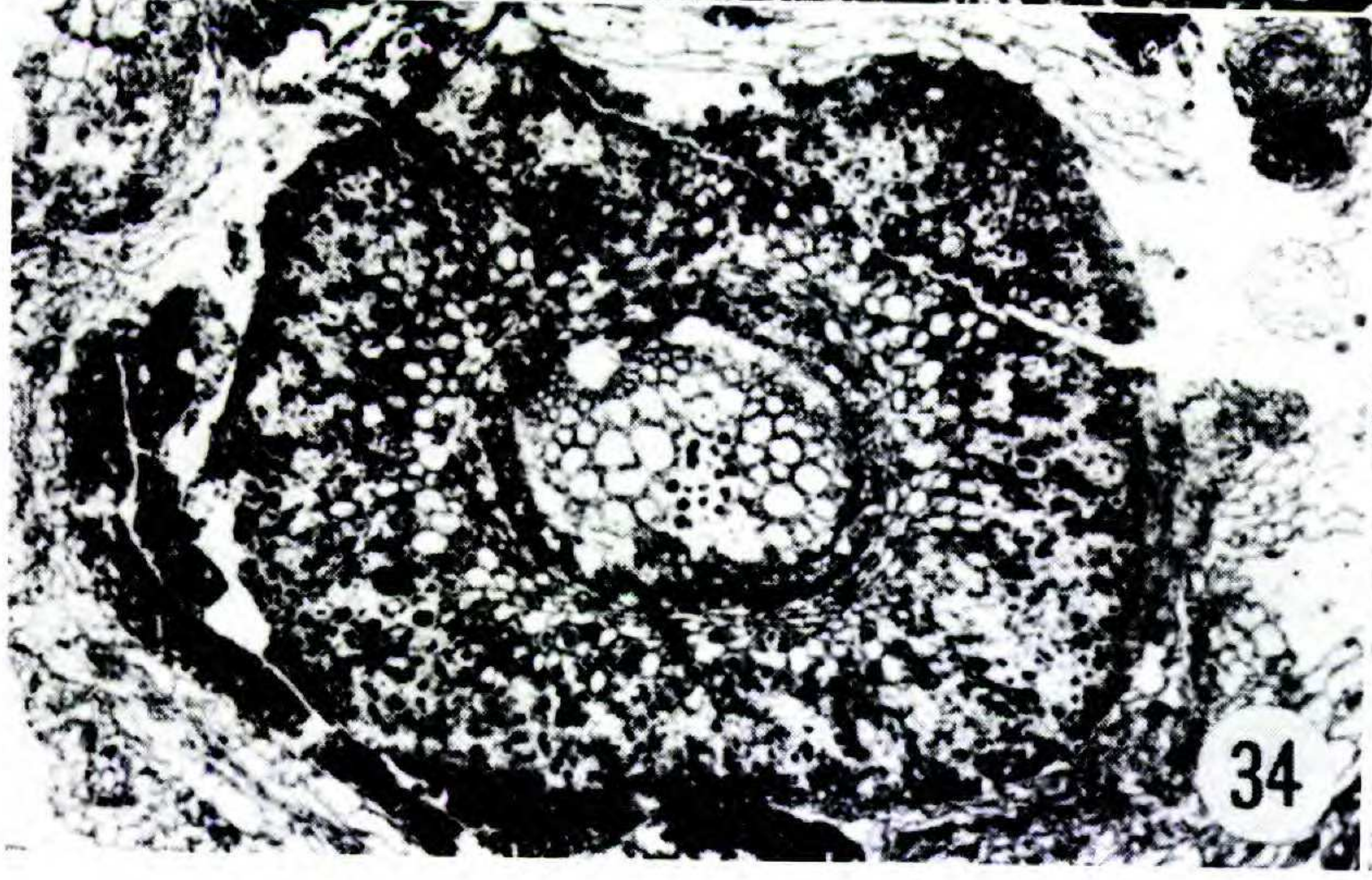
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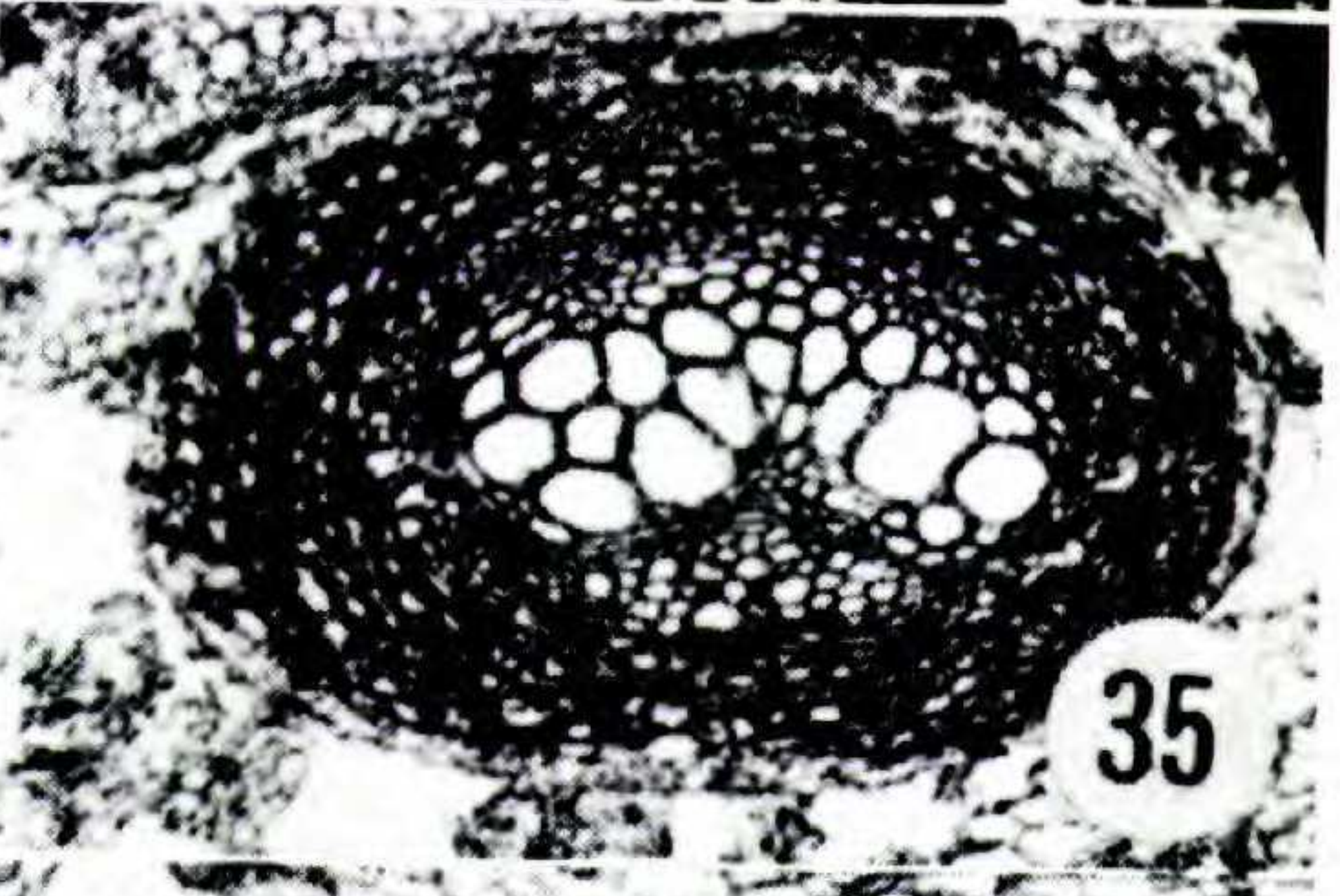
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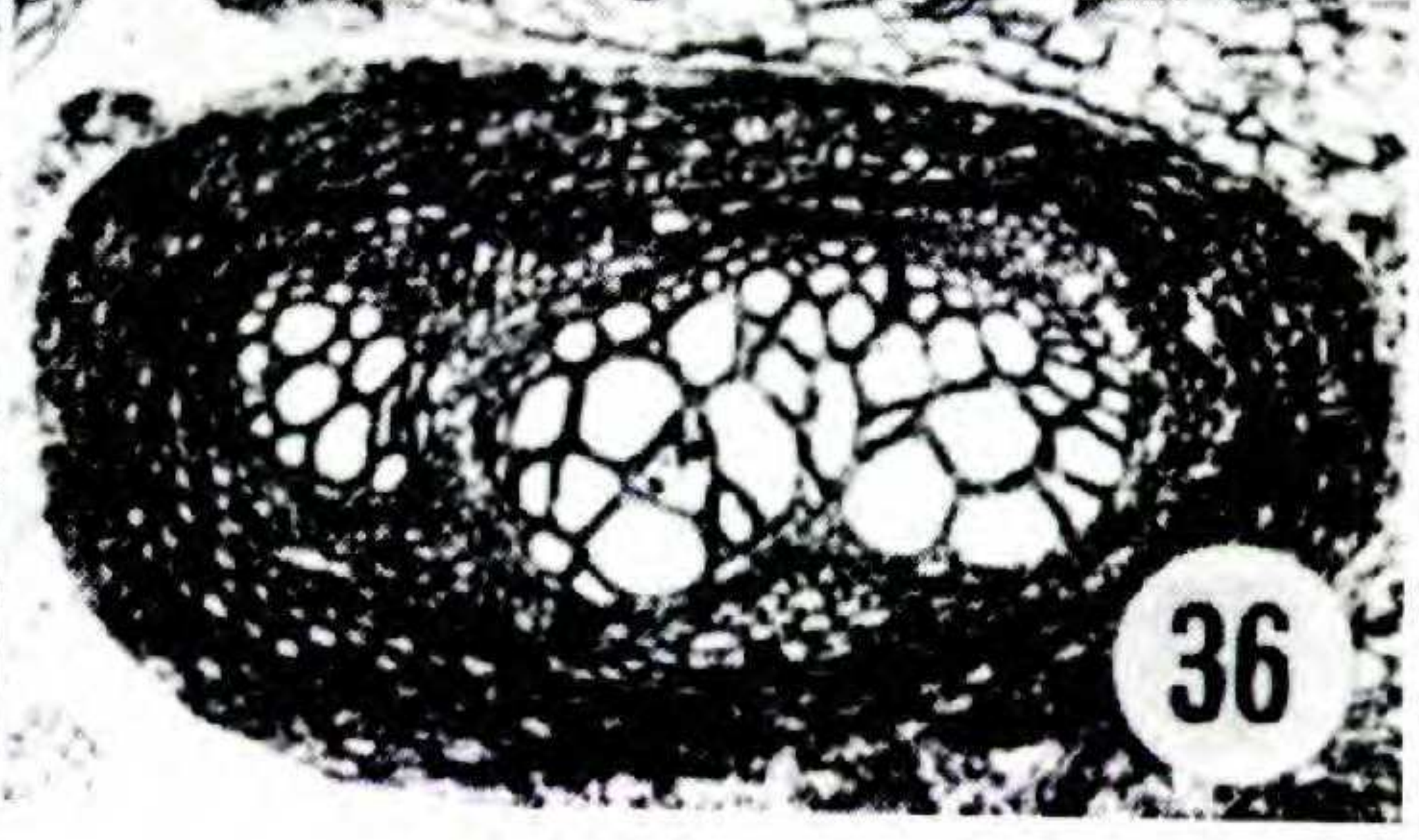
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Vitalization of the protostele with abundant parenchyma approaching a "mixed pith" in *Tubicaulis africanus* is a generally demonstrable trend in one phyletic line of *Tubicaulis* from the lower Westphalian A to the ?Upper Permian; parenchyma may be quite abundant in some older middle Pennsylvanian *Tubicaulis* stems (Fig. 40). A second evolutionary line leads to siphonostelic forms which occur in Middle Pennsylvanian forms of *Tubicaulis* and *Anachoropteris* and in larger stems of *Apotropteris minuta*; the appearance of a sclerotic or parenchymatous pith is transitory in some stems and apparently a mature feature of others (Figs. 52–55). Stelar anatomy will be discussed further with branching and foliar characters in appropriate groups of species of the Anachoropteridaceae.

PSALIXOCHLAENA—RHIZOME WITH SHOOTS

Branching of the larger stems (Fig. 28) of *Psalixochlaena cylindrica* is unequal with smaller lateral branches bearing the spirally arranged petioles (Figs. 31, 33), *i. e.* the rhizome bears shoots. The rhizome, its branch, and the first petiole are in the same plane in *Psalixochlaena*, and frequently only one petiole is developed on a lateral shoot (Figs. 32–33). Early (basalmost) stages of stem branching are identical to those of petiolar trace emission of some specimens (Figs. 29–30), and both types of branching are cross-sectionally similar to petiole emission in many *Botryopteris* species (Fig. 30, and see Holden, 1960, fig. 3, pl. 9). Holden (1960) established the abaxial curvature of the foliar strand at slightly higher levels (Figs. 34–36) and pointed out the similarity to foliar members of *Apotropteris* (Figs. 54–55). Foliar branching is apparently pinnate and circinate vernation was established by Holden (1960).

Typically, in anachoropterid foliar members with distinct protoxylem groups there are two protoxylem groups on the adaxial face and usually additional ones on each margin or side of the strand. The latter protoxylem groups follow pinna emission patterns and are decurrent with the nearest adaxial ones.

TUBICAULIS—STEMS WITH INVERTED C-SHAPED PETIOLAR XYLEM

Tubicaulis is an organ genus for terete, exarch protostelic stems without secondary xylem and with inverted C-shaped petiolar xylem traces (Mamay, 1952; Holden & Croft, 1962); *Anachoropteris* is an organ genus for isolated foliar members with inverted U- to C-shaped, to involuted xylarly strands.

Interconnections between *Tubicaulis* and *Anachoropteris* were first established (Hall, 1961) with a demonstration of the transition from typical *Tubicaulis* petioles to foliar anatomy of the *Anachoropteris involuta* type (Figs. 40–43E). Hall (1961) also reported the occurrence of a lateral bud on a foliar member of the *A. involuta* type (Fig. 48). By priority, specimens showing *Anachoropteris* anatomy are assigned to that genus, but it is not clear if the phyletic line of

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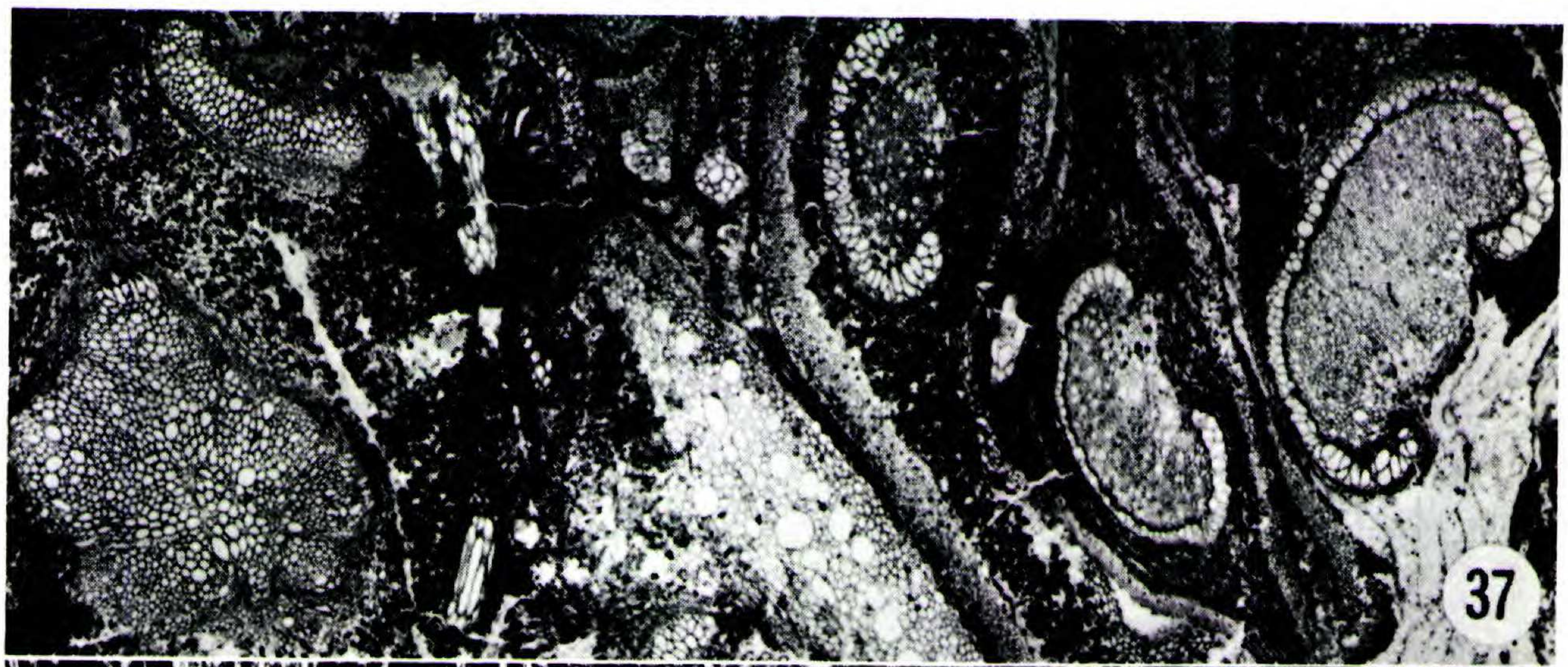
FIGURES 28–36. *Psalixochlaena cylindrica* stem and frond anatomy. x.s. Halifax Coal, lower Westphalian A, England. × 25.—28. Stem.—29–30. Rhizome with lateral shoot trace (right).—32–33. Rhizome (Fig. 32), lateral shoot from rhizome and leaf trace (bottom).—34–36. Foliar members.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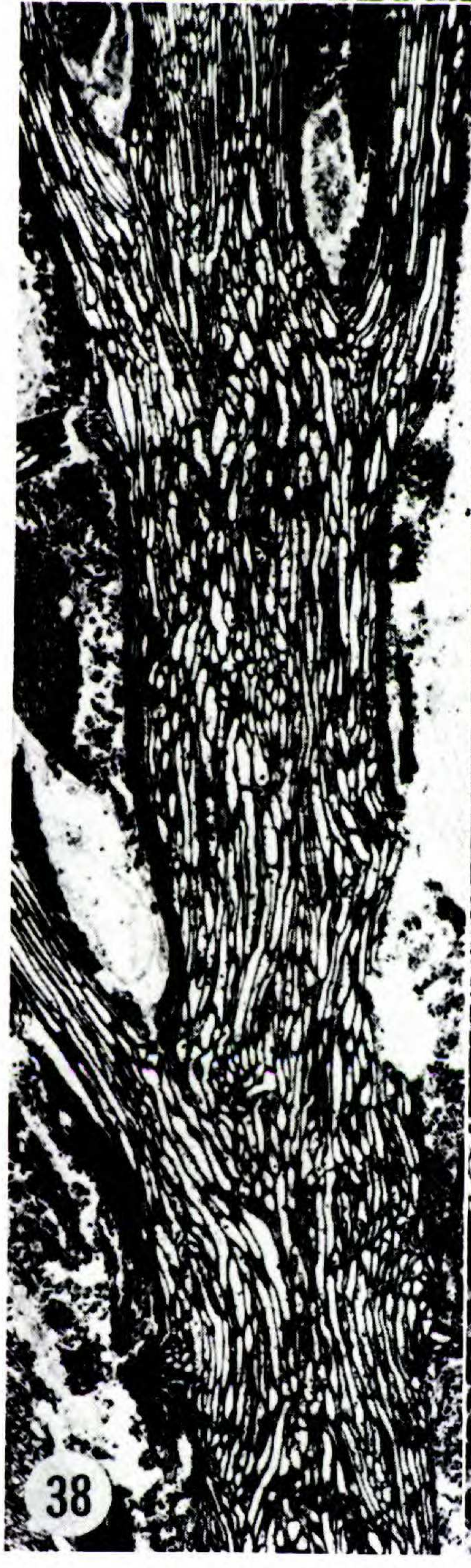
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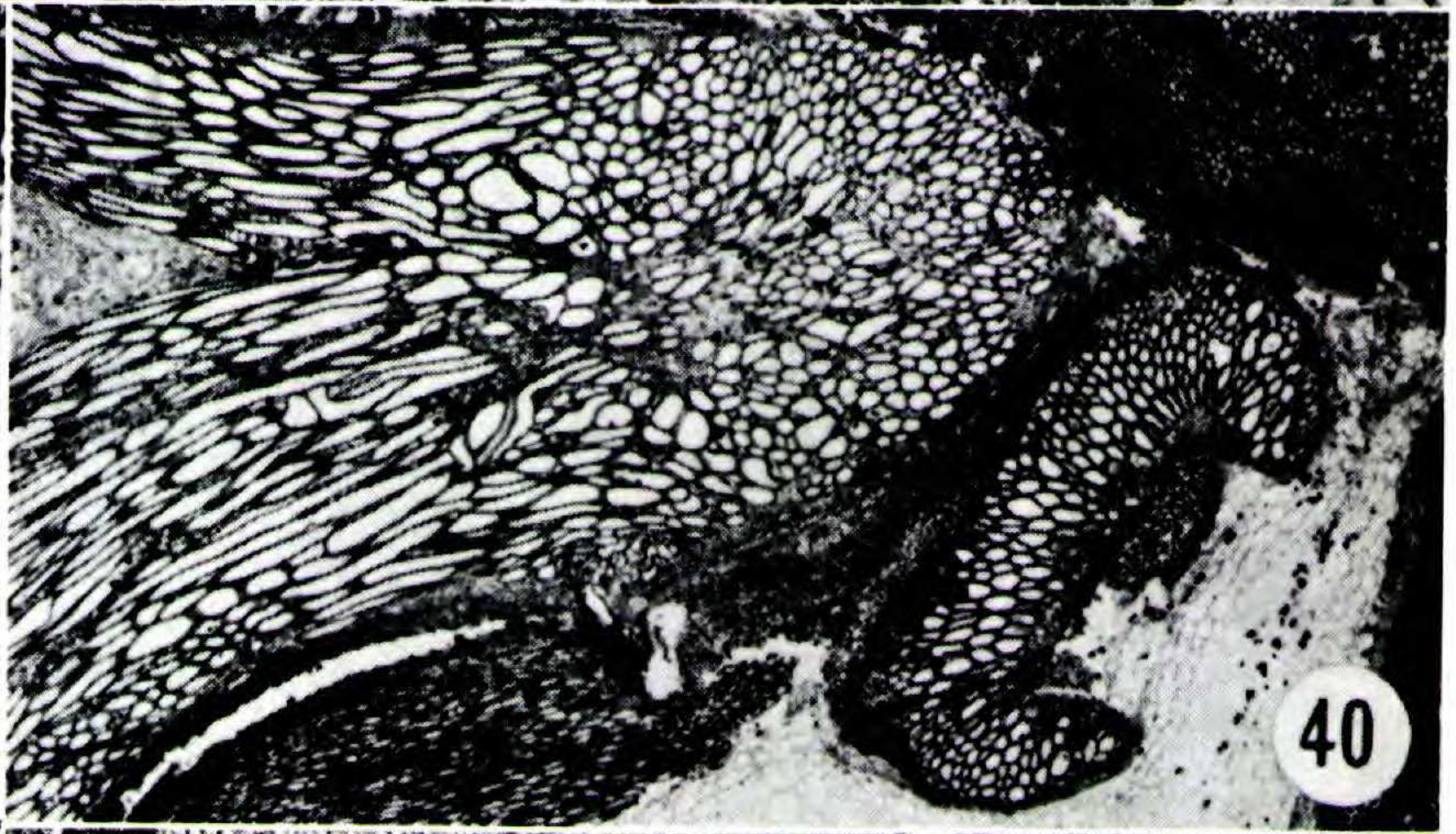
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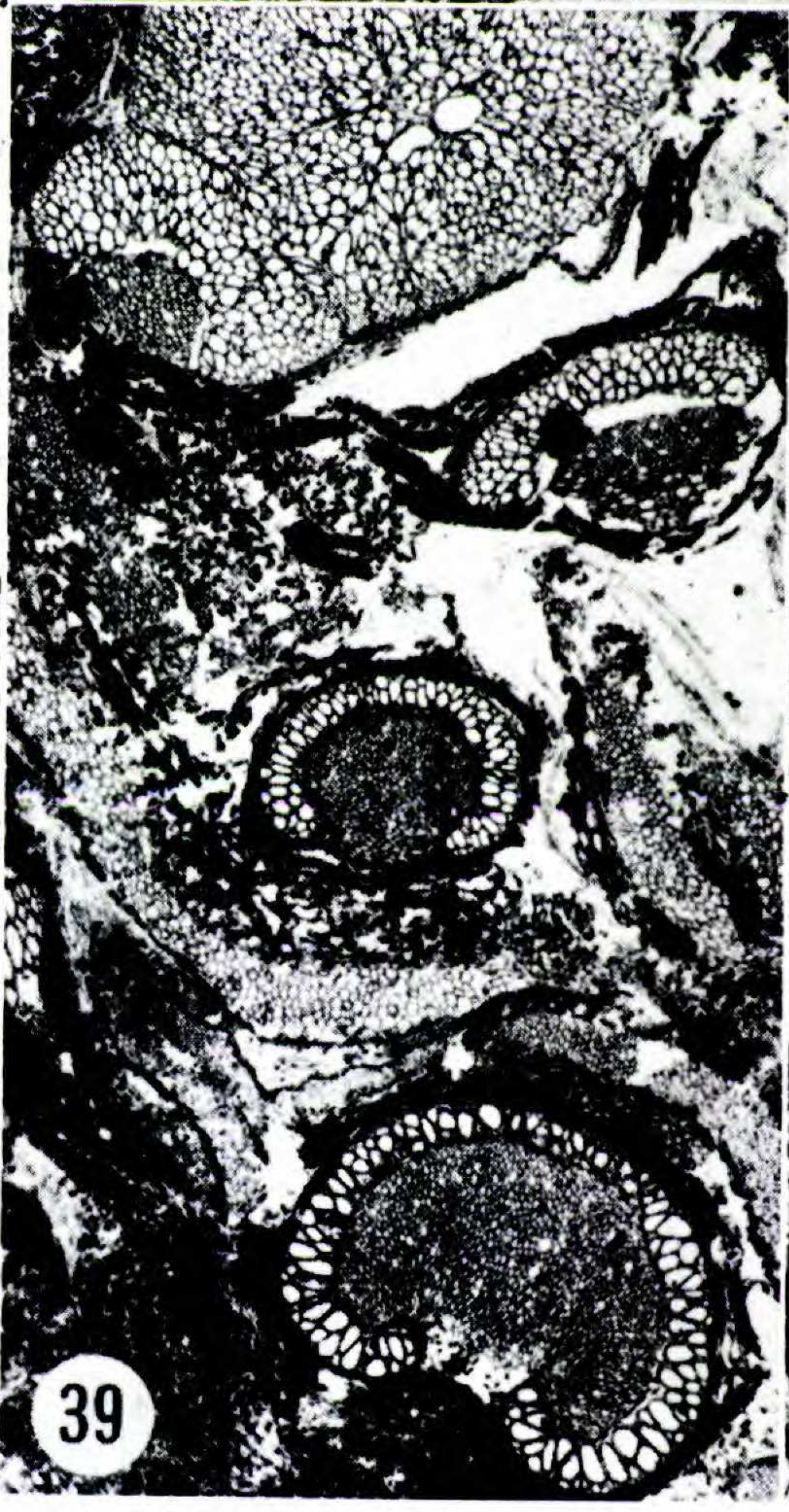
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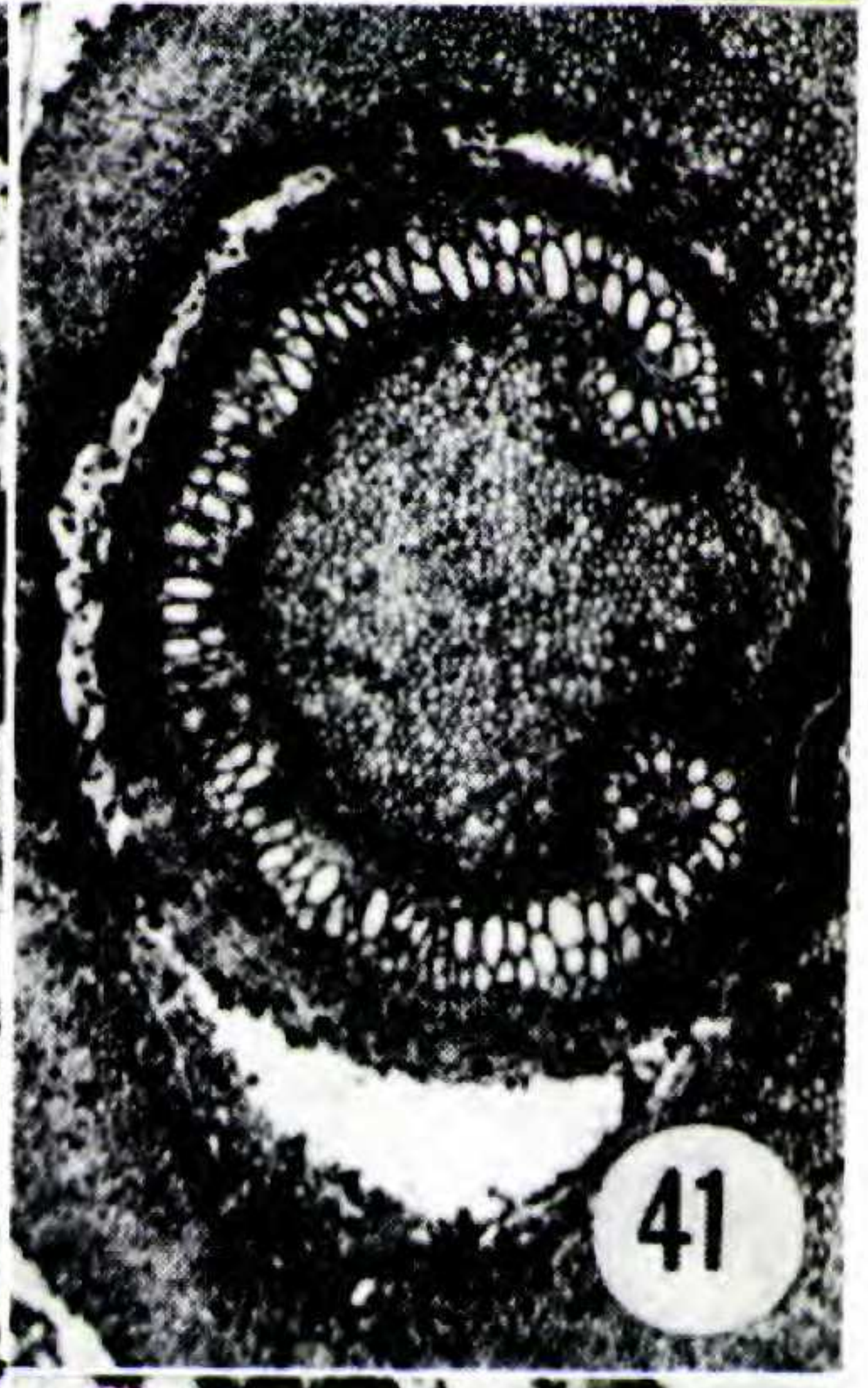
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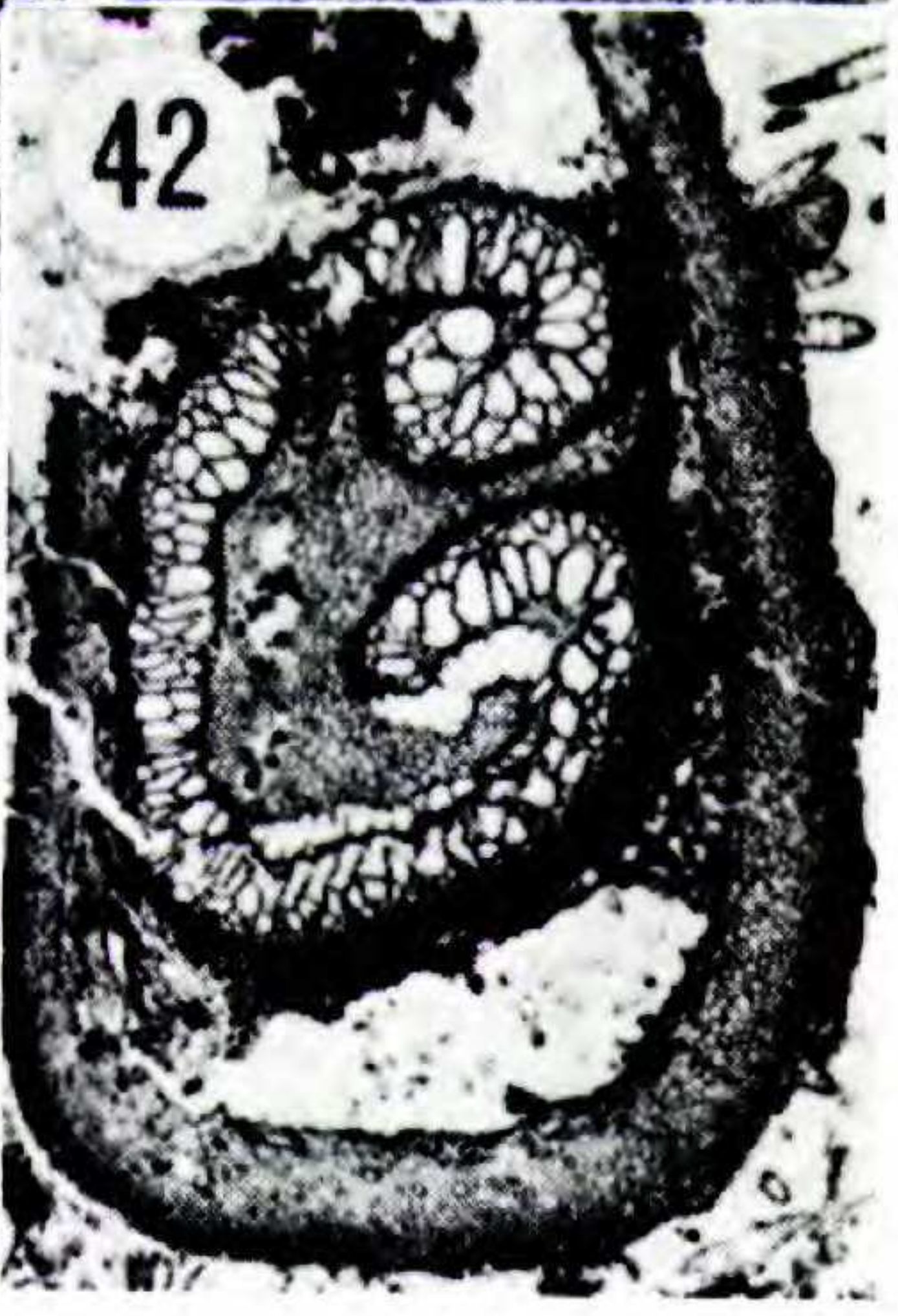
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Tubicaulis species with vitalized protosteles are the only ones bearing *Anachoropteris* fronds or where generic limits will ultimately fall among such assembled plants. *Tubicaulis* stems with vitalized protosteles also occur on *Anachoropteris* fronds. Vegetatively, there are fairly coherent branching patterns and types of stelar anatomy to summarize for specimens showing both *Tubicaulis* and *Anachoropteris* morphology.

With the same stem and petiolar organization there are at least two major evolutionary lines of *Tubicaulis* (Eggert, 1959*b*) from the lower Westphalian A to the Permian, and each exhibits the same kinds of diversity in habit and size. The stelar characters of the two groups are mixed protosteles with multiseriate scalariform metaxylem pitting compared to solid protosteles with reticulate to multiseriate circular bordered pitting (*T. sutcliffia*, *T. berthieri*, and *T. solenites*). Among the seven named species of *Tubicaulis* there are also marked differences in size, habit, and cortical anatomy. Some *Tubicaulis* species were erect to semi-erect; others were epiphytic to scrambling. An epiphytic habit for *T. scandens* was suggested by Mamay (1952), who summarized other data on *Tubicaulis* as have Eggert (1959*b*) and Holden and Croft (1962). Permian species, *T. africanus* from Tanganyika and *T. solenites* from East Germany, have the largest stem diameters (4.5–14.0 cm) and their steles are 3.5–6.0 mm in diameter.

Tubicaulis stems with mixed protosteles, suggesting progressive increase in parenchymatization of the xylem, are an unnamed species from the lower Westphalian A of England (Millay, 1970), several Middle Pennsylvanian species (Figs. 37–40) including *T. multiscalariformis* (Delevoryas & Morgan, 1952), *T. stewartii* from the Upper Pennsylvanian (Eggert, 1959*b*) and *T. africanus* from the Permian (Holden & Croft, 1962). Vertical anastomosing strands of parenchyma partially divide tracheidal groups, and abundant parenchyma may appear in the center as a "mixed pith" with scattered tracheids; there are interconnections with parenchyma extending to the outer xylary margin (Holden & Croft, 1962).

ANACHOROPTERIS—FOLIAR MEMBERS AND BRANCHING

Anachoropteris is based on a foliar member (*A. pulchra*) with abaxial curvature and an inrolled (involute) vascular strand differing from the C-shaped xylem of *Tubicaulis* species. More than a dozen species have been described (Corsin, 1937; Graham, 1935; Hoskins, 1930) ranging from *A. williamsonii* in the lower Westphalian A to *A. involuta* types in the Lower Permian. Two series of species are recognized (Corsin, 1937). The *A. robusta* series includes numerous distinct foliar members with variously arched to U- and almost

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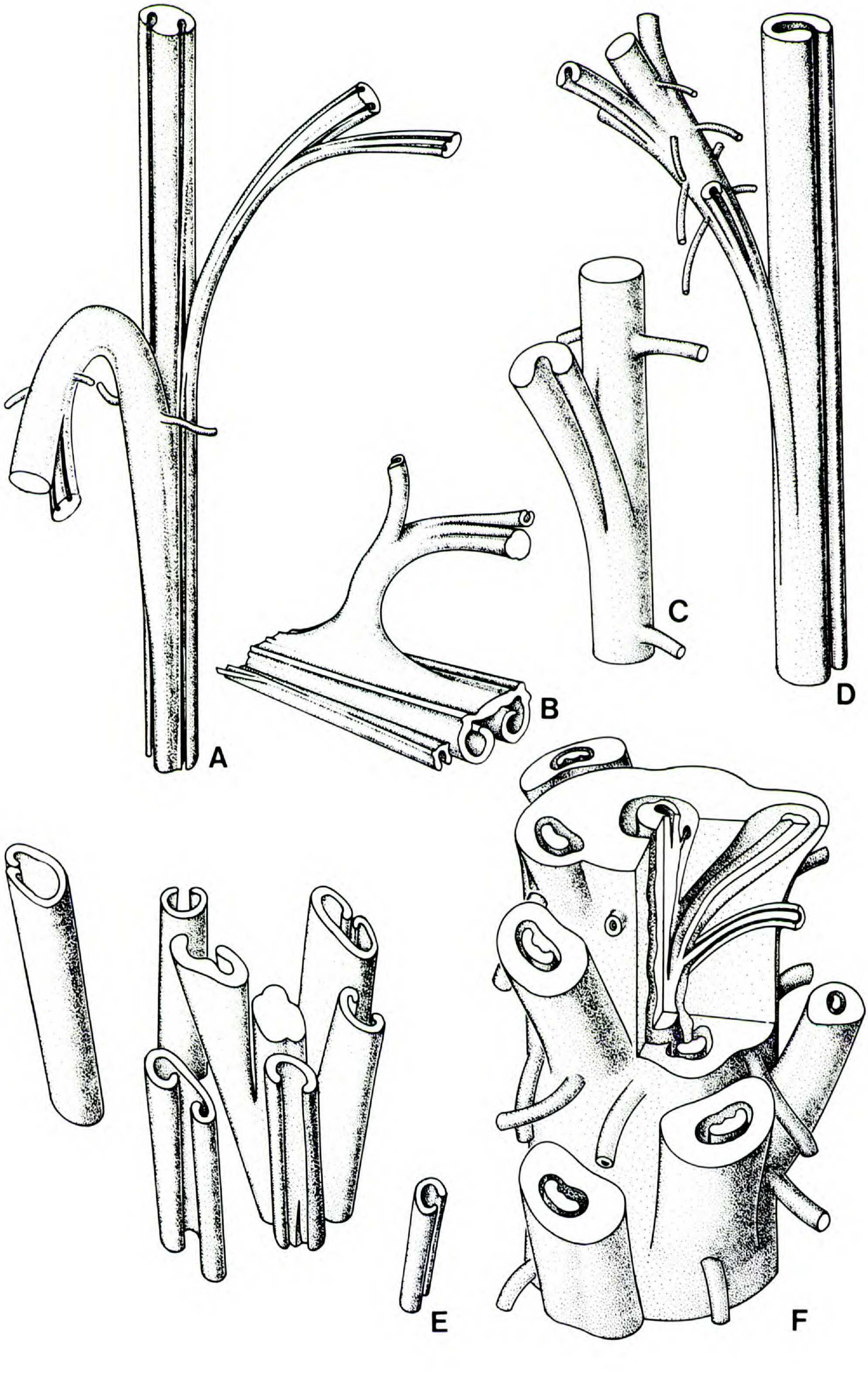
FIGURES 37–42. *Tubicaulis* and *Anachoropteris* anatomy. × 10.—37. Stem and petiolar traces x.s. Lower Cherokee Group, Iowa.—38–39. Longitudinal and cross-section of rhizome with petiolar traces. Herrin Coal, Illinois.—40–42. Rhizome stele and petiolar strands in x.s. at successively higher levels to the *Anachoropteris involuta* type foliar member (Fig. 42). Murphysboro Coal Equivalent, Indiana.


A
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E
F

C-shaped vascular strands in cross-section; the *A. involuta-A. williamsonii* series includes those species with inrolled xylary margins and is a heterogeneous group of taxa with very similar cross-sectional anatomy. Within the *A. involuta* group there are at least three distinct branching types in the development of shoots on fronds. Pinnately compound fronds bear protostelic shoots laterally (Fig. 48) and adaxially (Figs. 43B, 47); foliar branching is also dichotomous with pinnate lateral divisions, and siphonostelic to protostelic shoots are formed by dichotomy of the frond (Fig. 51).

Pinna trace formation in *A. involuta* type fronds consist of lateral extra-marginal development of C- to O-shaped pinna traces (Figs. 44–45). In addition to the C-shaped to involuted foliar xylem configurations exhibited by the *Tubicaulis* type petioles and *A. involuta* foliar members (Figs. 39–42), there are other configurations which ontogenetically continue from the involuted stage in a somewhat different anachoropterid frond. The fronds which exhibit dichotomous branching and bear siphonostelic shoots exhibit an involute xylary strand in part and, also have stages with the inrolled arms laterally joined to form a closed xylary configuration with inwardly projecting arm tips which, at higher levels, form a bar-shaped inner xylem strand (Figs. 46, 49).

Laminate pinnules with sporangia have been described in one species with *Anachoropteris* foliar anatomy, and the genus *Sermaya* is the basis for a new family (Eggert & Delevoryas, 1967).

Anachoropteris clavata has a U-shaped xylary strand with expanded club-like abaxial arms (Graham, 1935). The stem has a solid protostele. The study of this Middle and Upper Pennsylvanian species by Delevoryas and Morgan (1954*b*) provided the first evidence of the stem of *Anachoropteris*, established the actual abaxial curvature or inverted orientation of the petiolar trace to the stem, and was the first report of shoots on foliar members in the Anachoropteridaceae (Fig. 43D). Shoots also occur on foliar members of the *Anachoropteris involuta* type, and there is a parallel with *Botryopteris* in the kinds of branching, with both lateral and adaxial protostelic shoots (Figs. 43, 47–48, 50). *Anachoropteris involuta* type fronds also exhibit dichotomies with one member of the division becoming a siphonostelic shoot (Figs. 51–53). The siphonostele trace is formed by closure of the arched xylary portion associated with involute foliar anatomy, and a massive development of tracheids takes place around a sclerotic pith which corresponds histologically to inner ground tissue usually seen within such foliar xylem strands. The extent of such siphonostelic anatomy

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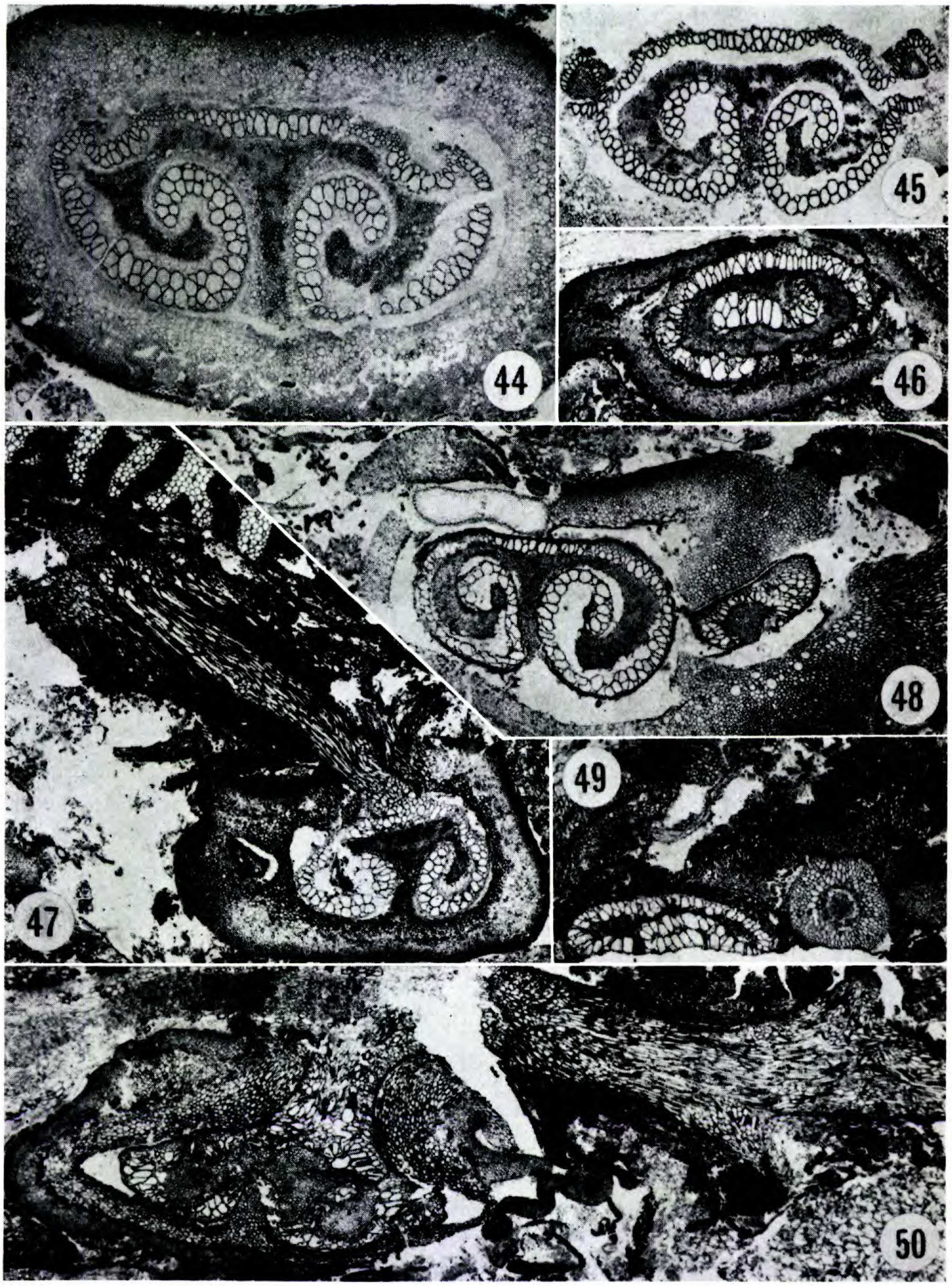
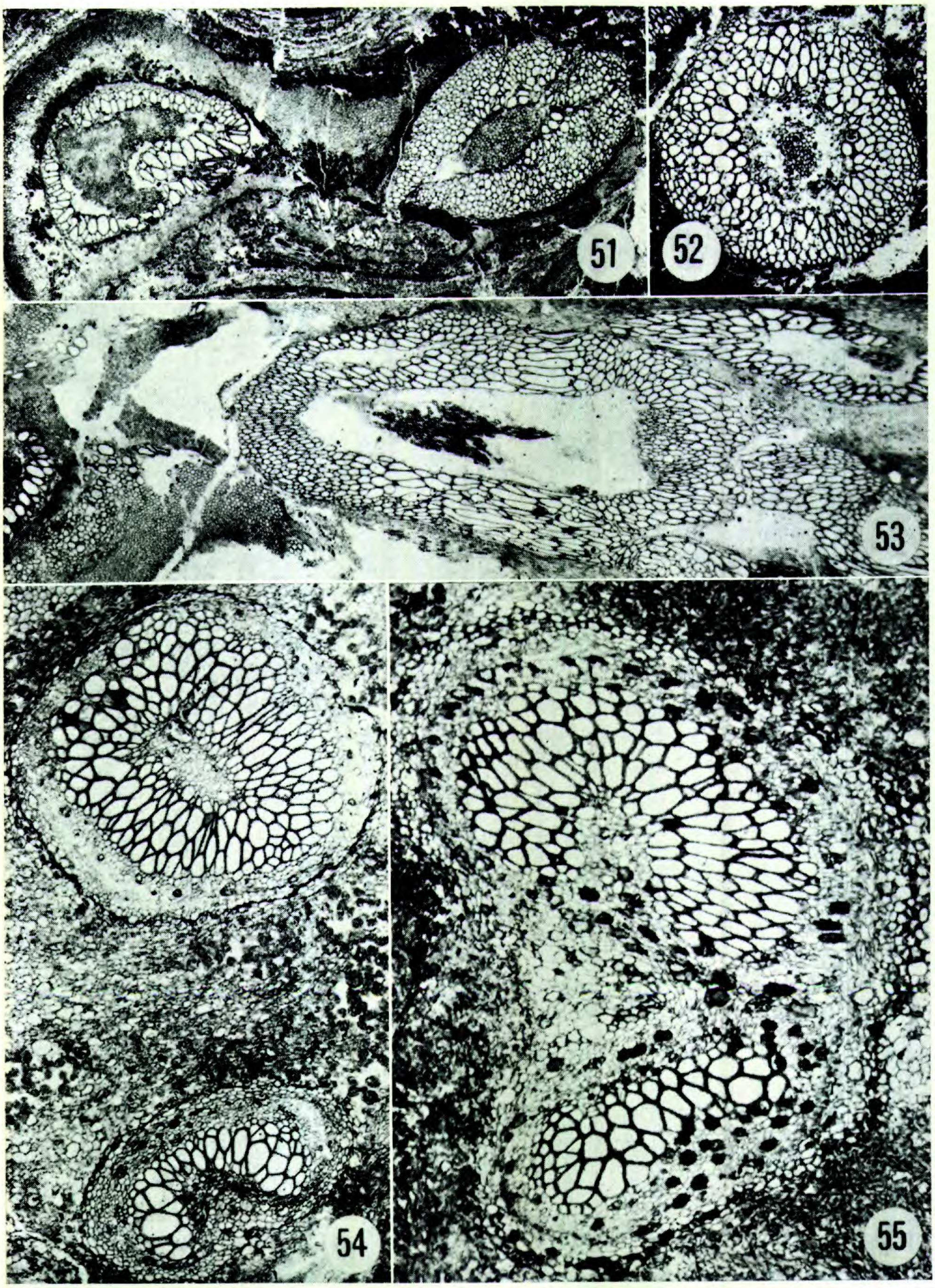
FIGURE 43. Xylary reconstructions of branching in Pennsylvanian age coenopterid ferns.—A. *Botryopteris* sp. with adaxial shoot and lateral pinna on foliar member.—B. *Anachoropteris* sp. with adaxial shoot (roots deleted) and lateral pinna on foliar member.—C. *Apotropteris minuta* with petiolar trace departure from stem (redrawn from Morgan and Delevoryas, 1954).—D. *Anachoropteris clavata* with lateral shoot on foliar member (redrawn from Delevoryas and Morgan, 1954*b*).—E. Stem (roots deleted) of *Tubicaulis* sp. bearing petioles of *Anachoropteris involuta* type (redrawn from Hall, 1961).—E. Portion of shoot of *Catenopteris simplex* with cortical tissues represented (redrawn from Phillips and Andrews, 1966).



FIGURES 44–50. Branching of anachoropterid foliar members. × 10.—44–45. *Anachoropteris involuta* with pinna trace formation, x.s. Parker Coal, Indiana. × 10.—46. Foliar member with closed elliptical xylem strand and internal xylary band. Herrin Coal, Illinois. × 10.—47. *Anachoropteris* sp. foliar member with lateral (left) pinna trace, x.s. and adaxial cauline trace, l.s. Herrin Coal, Illinois.—48. *Anachoropteris pulchra* foliar member in x.s. with lateral (right) pinna trace, in turn with cauline trace. Calhoun Coal, Illinois.—49. Foliar member and derived siphonostelic trace (right), x.s. Herrin Coal, Illinois.—50. *Anachoropteris* sp. foliar member, x.s. with adaxial shoot of *Tubicaulis* type in l.s. Herrin Coal, Illinois.



FIGURES 51–55. Siphonostelic stems of anachoropterid ferns.—51. Dichotomous branching of foliar member with closed foliar xylary strand (left) and siphonostelic trace. Herrin Coal, Illinois. × 10.—52. Siphonostele x.s. Herrin Coal, Illinois. × 25.—53. Oblique section of siphonostelic stage of *Tubicaulis* stem with petiolar traces. × 10.—54–55. *Apotropteris minuta* x.s. with siphonostelic stems (above) and leaf traces. Leaf gap in Fig. 55. Calhoun Coal, Illinois. × 25.

is apparently variable; a number of leaf traces pass off without effecting leaf gaps, and higher up there is a transition to a typical mixed protostele of the *Tubicaulis* type in some specimens. All the reported cases of shoots upon foliar members of *Anachoropteris* (Delevoryas & Morgan, 1954*b*; Hall, 1961) and those demonstrated herein also include pinna trace formation from the same foliar members.

APOTROPTERIS—SIPHONOSTELIC SHOOTS

Apotropteris minuta is an Upper Pennsylvanian fern originally described (Morgan & Delevoryas, 1954) as having a solid protostele in which a vertical indentation or groove occurs in the xylem above leaf trace departure (Fig. 43C). The foliar xylem is similar to that of *Psalixochlaena*. Small specimens of *Apotropteris minuta* are protostelic, and somewhat larger ones have a small pith (Figs. 54–55). There is a gradation of forms with a leaf gap (Fig. 55) and without a leaf gap. In the latter a decurrent funnel of parenchyma, adaxial to the leaf trace, joins the pith at a level below leaf trace departure. The indentation of xylem upon leaf trace departure reported by Morgan and Delevoryas (1954) may have been simply a leaf gap.

GRAMMATOPTERIS AND *CATENOPTERIS*—*INCERTAE SEDIS*

Some of the Paleozoic ferns suggest basic filicalean organization in the geometry of their foliar xylem and provide interesting parallels in stelar anatomy as possible prototypes, but not necessarily the actual progenitors, of extant families such as the Osmundaceae. *Grammatopteris*, *Catenopteris*, and a recently discovered Upper Pennsylvanian fern fall into the above category, and it seems desirable to treat them together as an *incertae sedis* group.

GRAMMATOPTERIS

Grammatopteris is known from stelar and leaf trace anatomy in *G. rigollotii* and *G. baldaufii* from the Stephanian and Lower Permian of Europe and has been reported also from the Visean of France, based on isolated foliar members assigned to *G. bertrandi* (Corsin, 1937). The foliar xylem in *Grammatopteris* is essentially a bar-shaped metaxylem strand in cross-section with adaxial protoxylem groups near each margin. The lack of curvature of the foliar xylem places this genus between the Anachoropteridaceae and Botryopteridaceae; stelar and cortical anatomy with the bar-shaped petiolar xylem traces of *G. baldaufii* have been considered as a possible link with the Osmundaceae (Miller, 1971). The solid protostele of the Lower Permian *G. baldaufii* exhibits broader shorter tracheids in the center surrounded by typical tracheids, a type of protostelic anatomy which occurs in some Upper Permian Osmundaceae (Thamnopteroideae) (Miller, 1971). Features of the anatomy of *Grammatopteris baldaufii*, which have also merited comparisons with the Osmundaceae are the distinct indentations in the stelar xylem, apparently relating to leaf trace departures, and scattered nests of sclerenchyma within the middle cortex as well as thick-walled cells in the outer cortex. Compared to the interpretation given to *G. baldaufii* by Sahni (1932*b*), the revised description of Renault's *G. rigollotii* differs markedly (Corsin, 1937). The solid protostele of *G. rigollotii* consists of a mixture of large and small tracheids with multiseriate bordered pitting, and the surrounding zone of tracheids in radial rows were interpreted as secondary xylem (Corsin, 1937). The tendency for identations along the xylary margin in *G. rigollotii* (as in *G. baldaufii*) was interpreted as undulations of the secondary xylem around departing leaf traces. The tracheidal diameters of the central primary xylem and those of the leaf trace xylem were larger than tracheids of the secondary xylem which surrounds the protostele and portions of departing leaf traces (see Corsin, 1937: 19, fig. 2).

CATENOPTERIS—C-SHAPED FOLIAR XYLEM

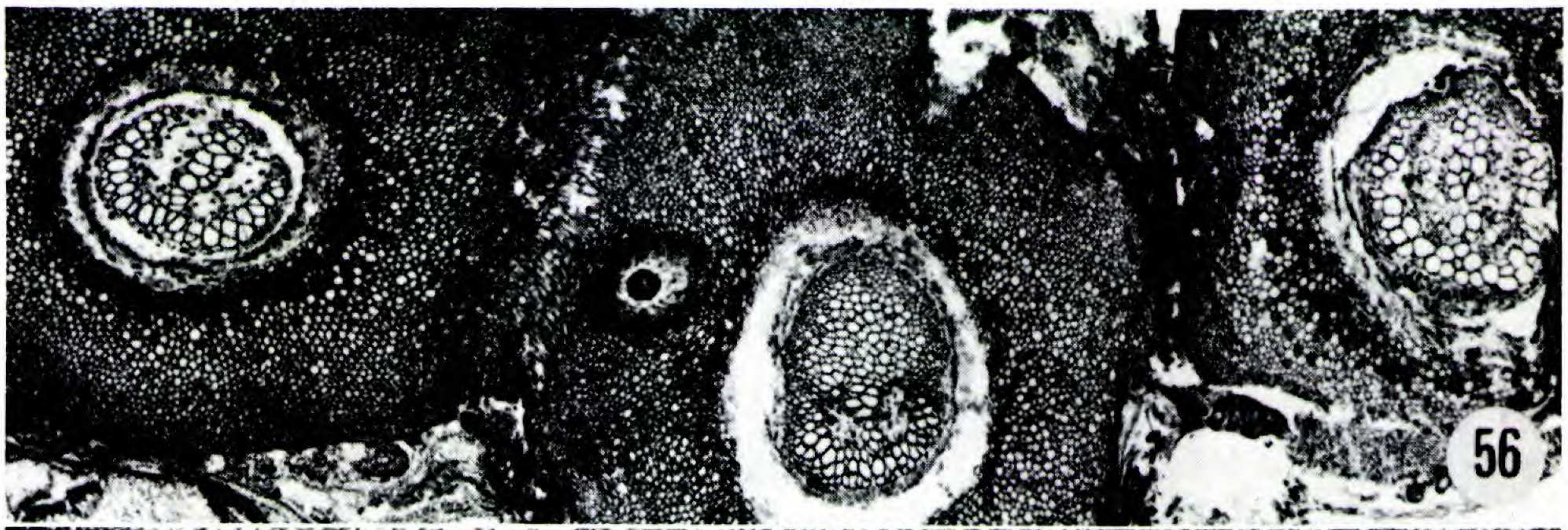
Catenopteris simplex is a small protostelic fern with adaxially curved shallow C-shaped foliar xylem similar to that of modern ferns such as *Osmunda* (Fig. 43E). Adaxial to each leaf trace is a decurrent lens of parenchyma extending down into the solid protostele which has scalariform metaxylem (Phillips & Andrews, 1966). In addition to roots from the stem a root occurs on the abaxial face of each leaf trace. *Catenopteris* in the Upper Pennsylvanian has been the only known coenopterid fern until recently with a simple catenalean C-shaped foliar xylem strand. Another fern with C-shaped foliar xylem and a siphonostelic stem has been discovered recently from the Upper Pennsylvanian of Indiana. To the extent that sectioning has progressed a leaf gap apparently occurs above leaf trace departure.

BOTRYOPTERIDACEAE

BOTRYOPTERIS—WHOLE PLANT GENUS

Among coenopterid genera with numerous species, *Botryopteris* with more than ten appears to be a natural assemblage and a prime example of a genus through geologic time (Visean to Permian) with diverging coherent phyletic lines. Vegetative species have been based on stratigraphically disjunct forms emphasizing changes in anatomy and geometry. For example, *B. tridentata* is separable from *B. ramosa* largely on the basis of its siphonostelic stem (Figs. 79–80) at the Westphalian A-B boundary; *B. ramosa* occurs in the lower Westphalian A. At higher stratigraphic horizons *B. tridentata* foliar members have more prominent adaxial xylary ridges than *B. ramosa* (Figs. 63–65F, G).

Botryopteris is known from over 30 stratigraphic horizons in the Pennsylvanian of the U.S.A., western Europe and the Donetz Basin of the U.S.S.R., and the same species occur across these areas in coal balls and other petrifactions of stratigraphically similar ages. *Botryopteris tridentata* is known from the U.S.S.R. (Snigirevskaya, 1961, 1962), West Germany (Felix, 1886), and across the U.S.A. from Kentucky to Kansas. The recent study by Galtier (1971) of the type material of *B. forensis* from France (Renault, 1875) allows recognition of the same species in the U.S.A., described under the names of *B. americana* (Figs. 56, 65D–E, 73), *B. trisecta* (Figs. 65H, 69, 70), and in part specimens assigned to *B. globosa* (Graham, 1935; Mamay & Andrews, 1950; Delevoryas & Morgan, 1954*a*; Murdy & Andrews, 1957; Phillips 1961, 1966; Phillips & Rosso, 1970).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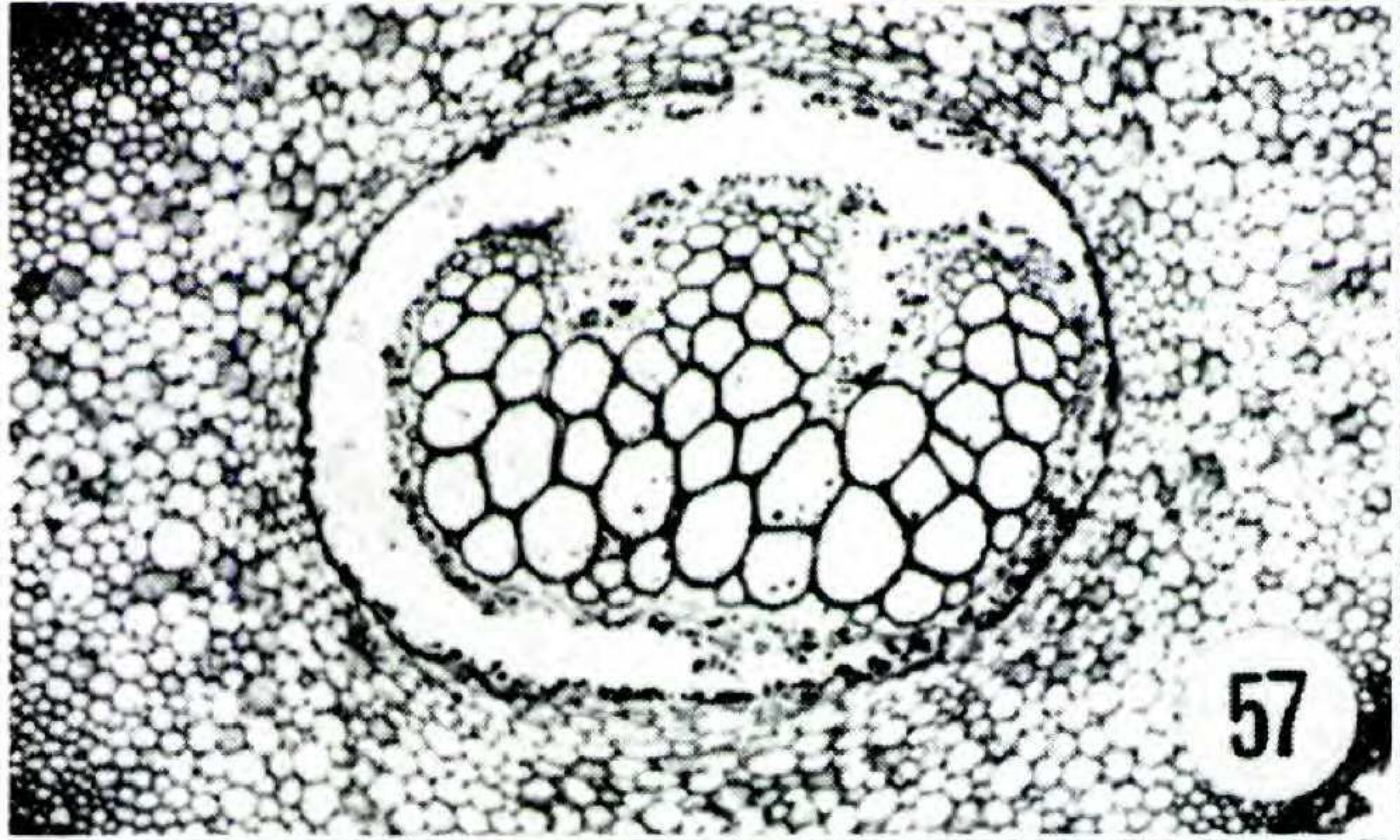
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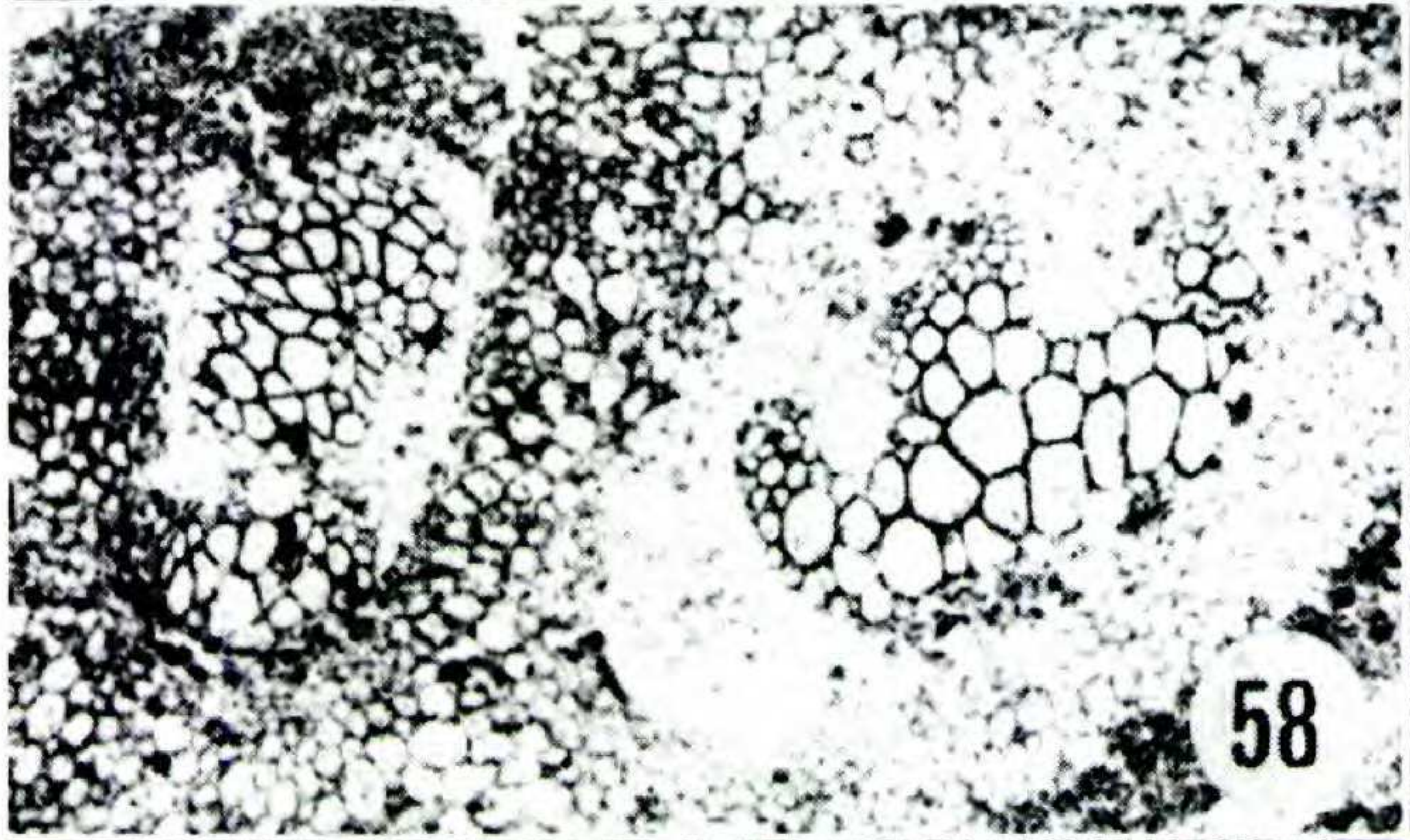
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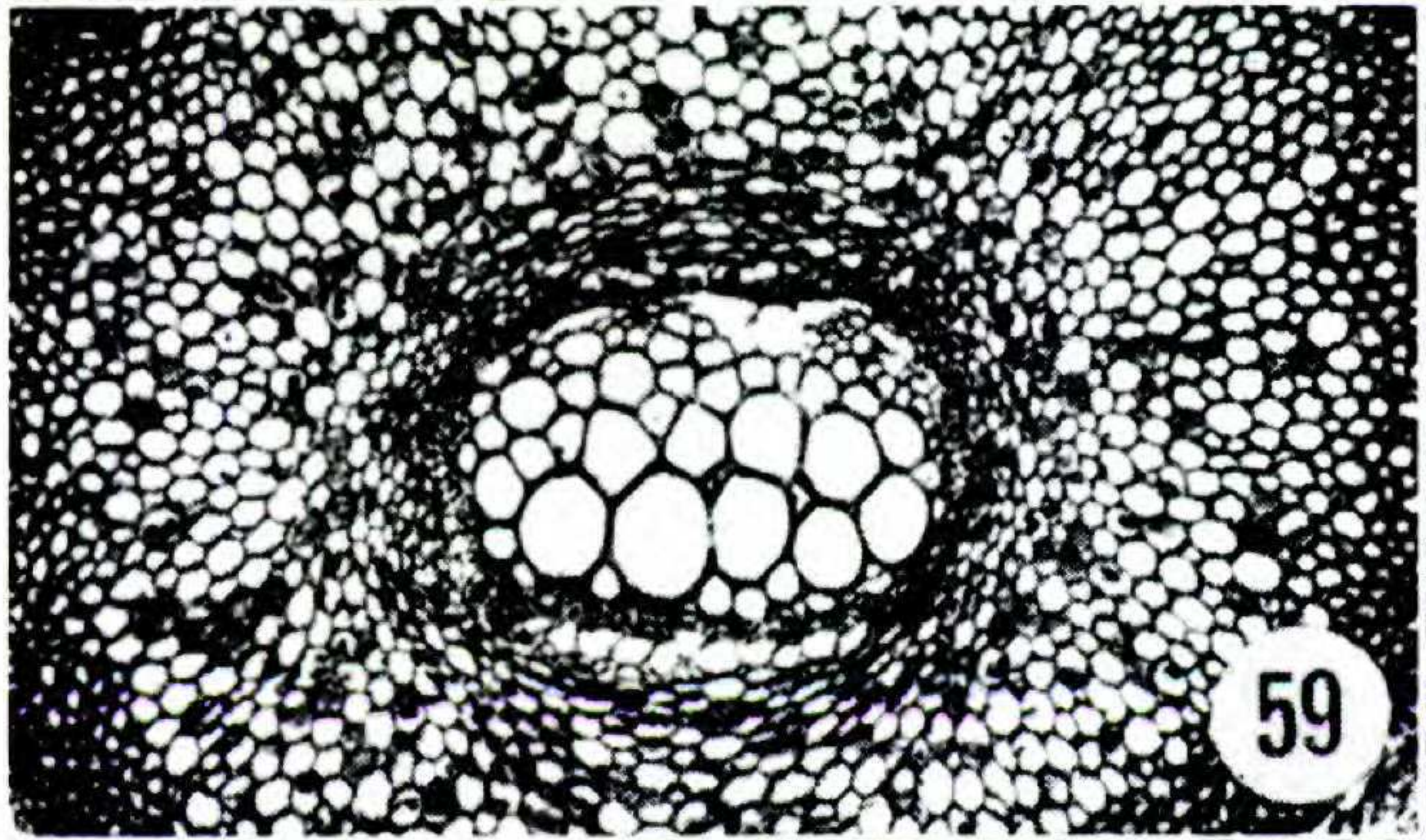
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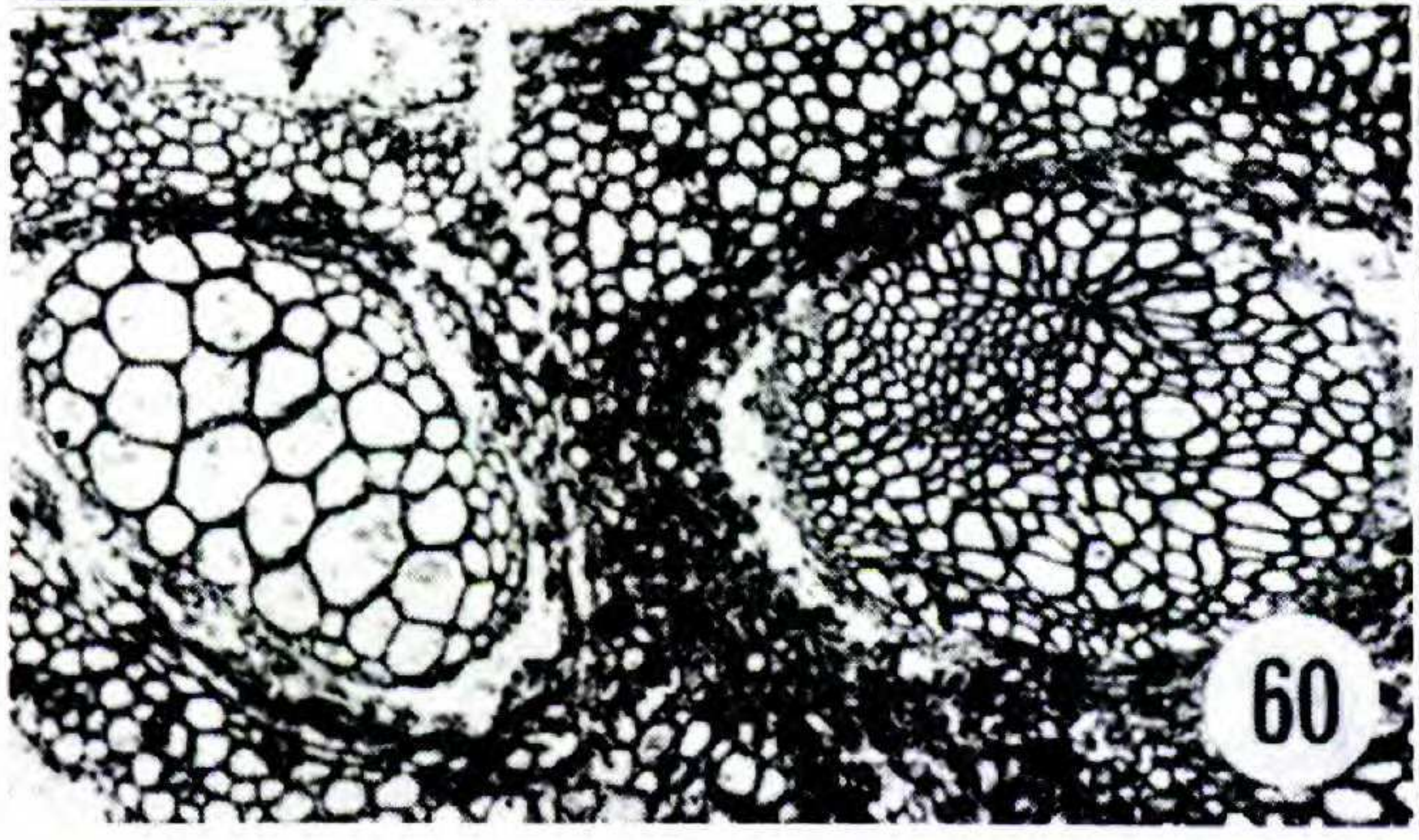
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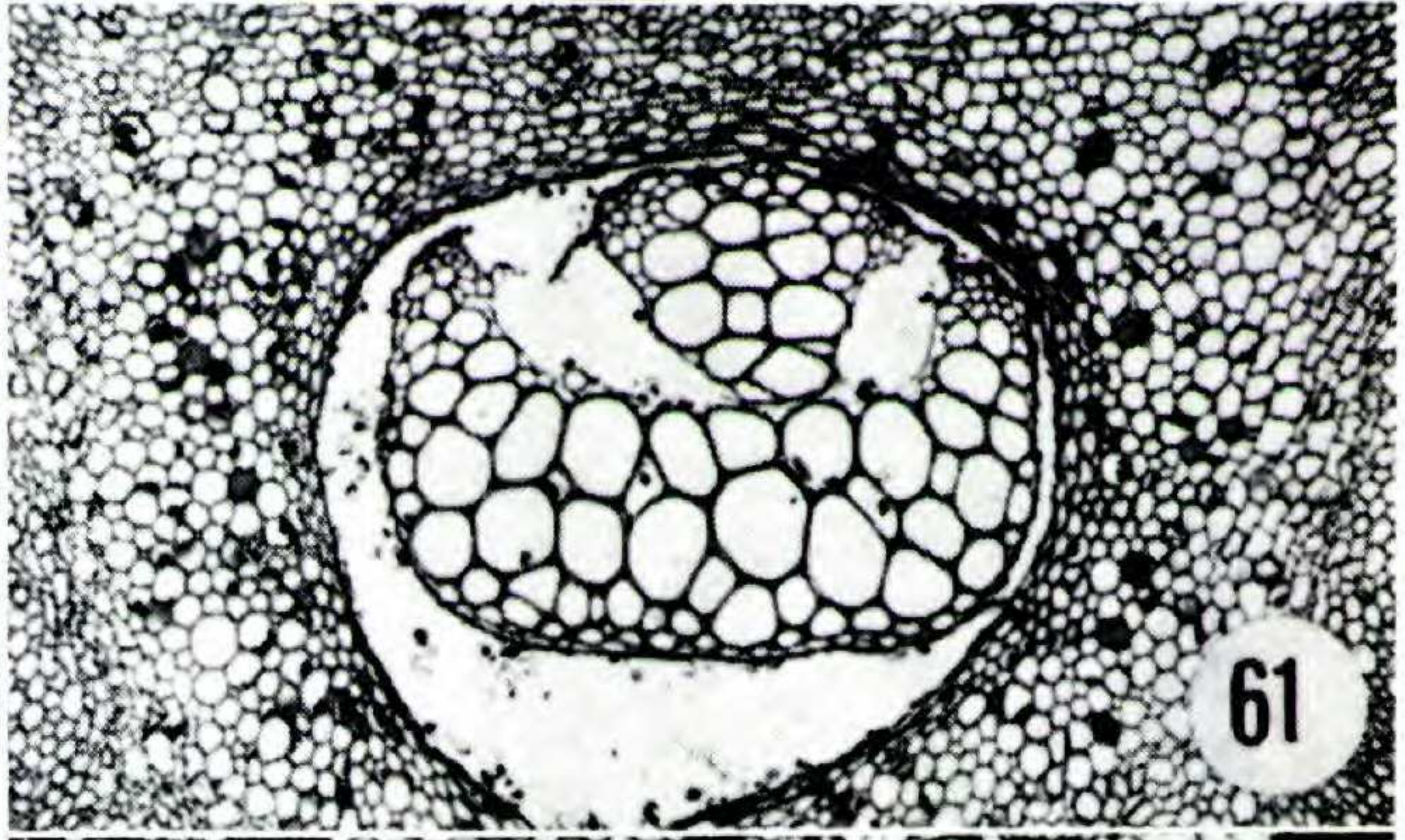
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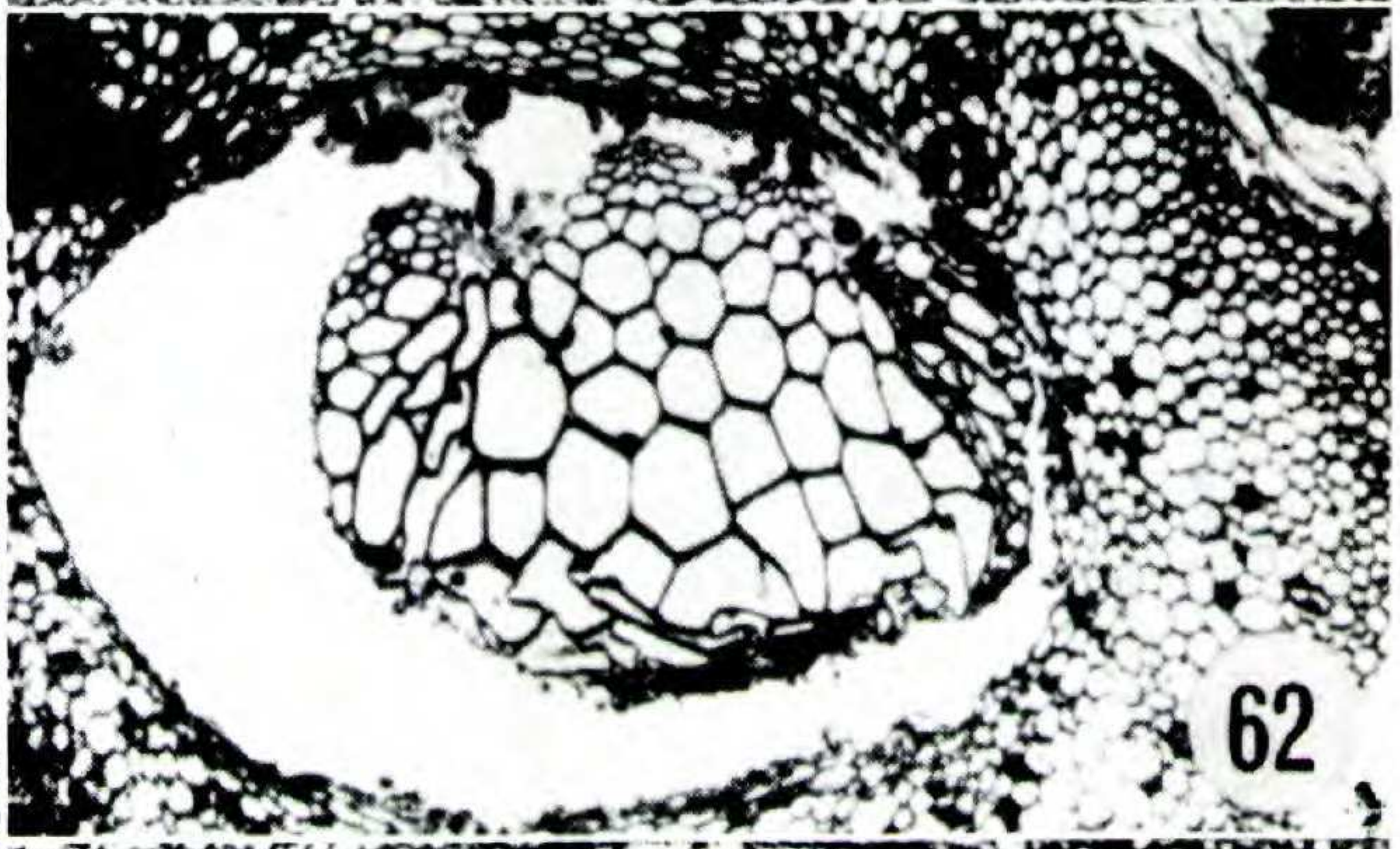
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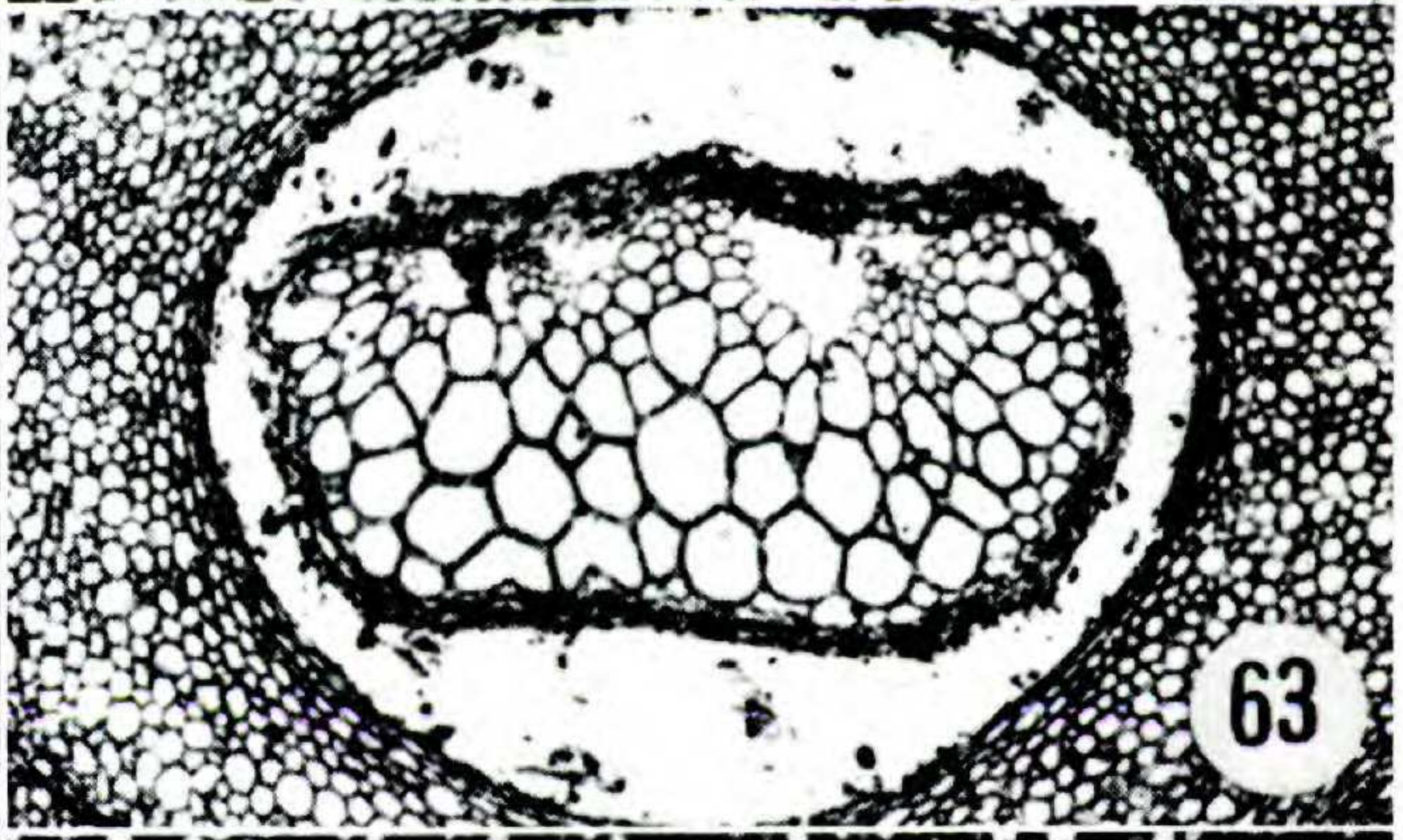
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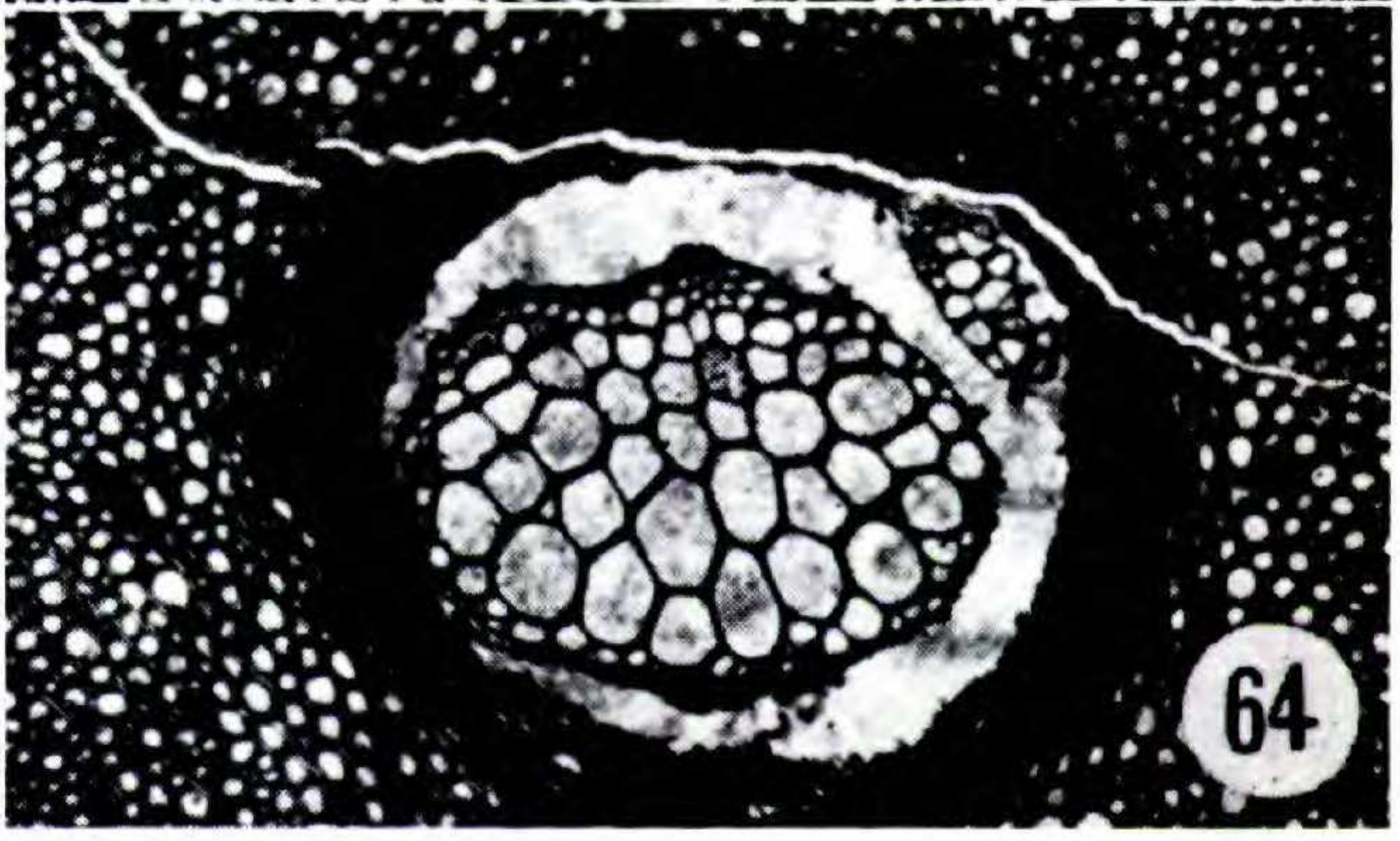
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Three divergent phyletic lines of *Botryopteris* evolved between the earliest appearing Visean assemblages of *B. antiqua* (Fig. 60), and the lower Westphalian A species, *B. hirsuta* (Fig. 59), *B. ramosa* (Fig. 64), and *B. mucilaginosa* (Fig. 62). These three specific epithets are convenient designations for the phyletic lines; a fourth, anatomically simpler, line parallels these and is designated the "pseudoantiqua" line (Fig. 66). The *B. hirsuta* line includes *B. forensis* and intermediate forms which have not been described yet (Figs. 57–58); in the *B. mucilaginosa* line is an undescribed Middle Pennsylvanian species (Fig. 61) and also the Stephanian *B. renaultii* (Corsin, 1937); *B. tridentata* is allied with *B. ramosa.*

The common anatomical features of the foliar members of *Botryopteris* are the somewhat elliptical vascular strand in cross-section with protoxylem located always medianly on the adaxial face and at some stage with lateral adaxial protoxylem groups which are associated with lateral divisions. The evolutionary changes in foliar xylem configurations from a *B. antiqua* type are the progressive decurrence of lateral protoxylary groups to a median group of protoxylem and the elaboration of xylem geometry (cross-sectional) into three adaxial ridges and finally into three adaxial xylem arms (Figs. 56–64). The appearance of adaxial xylary ridges or arms establishes an adaxially curved strand in most species of *Botryopteris*, but the primitive ellipsoidal configuration occurs across the Pennsylvanian in the "pseudoantiqua" line (Figs. 66–68).

Bilateral symmetry, pinnate branching, circinate vernation, sporangia-bearing, laminate pinnule-bearing, and phyllotactic arrangement of foliar members on shoots collectively attest the foliar interpretation given them. Apart from the bearing of fronds, *Botryopteris* stems are not known to branch, with the possible exception of *B. mucilaginosa* (Kraentzel, 1934). Shoots occur on the fronds in *Botryopteris* and effect vegetative propagation.

Branching patterns of the fronds of *Botryopteris* provide distinctions among the three divergent lines. Fronds are pinnately branched and have both pinnae and shoots. In the *B. mucilaginosa* line the shoots are borne adaxially (Figs. 43A, 72, 77) as in some *Anachoropteris involuta* types (Fig. 43B). In the other phyletic lines shoots are lateral, occurring along various orders of the frond except in laminate and fertile portions; the shoots occupy positions comparable to pinnae or at the bases of foliar members. The details of lateral cauline trace formation differ in the *B. hirsuta* and *B. ramosa* lines (Fig. 65); minor differences occur within each concomitant with changes in xylary configurations.

Frond morphology in *Botryopteris forensis* consists of a pinnately compound

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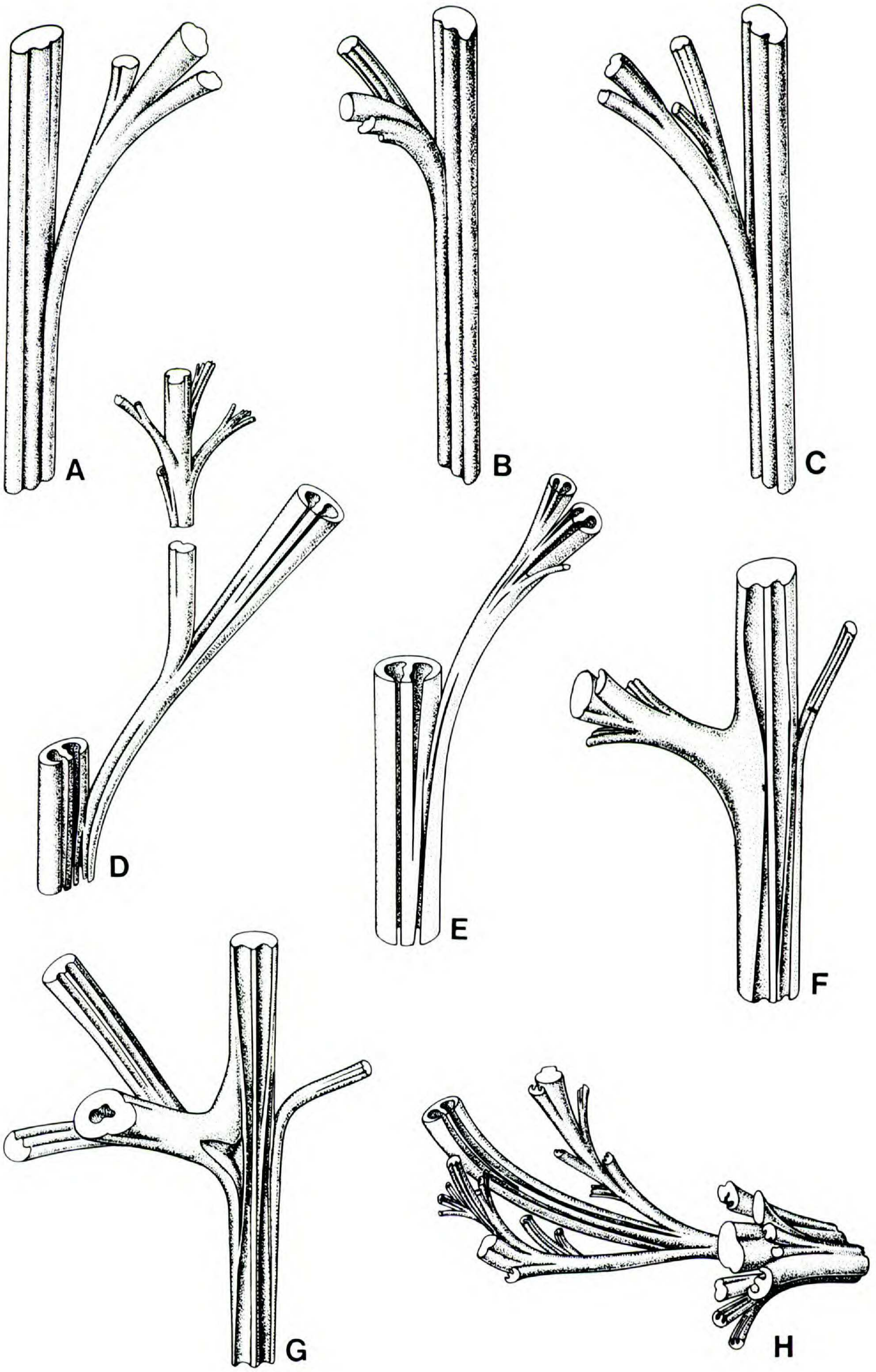
FIGURES 56–64. Foliar members of *Botryopteris* in x.s. × 25 except Fig. 56.—56. *B. forensis* with rachis (right), primary pinna (left) with shoot bearing petiolar trace. Calhoun Coal, Illinois. × 10.—57. *Botryopteris* sp. Pottsville Group, Kentucky.—58. *Botryopteris* sp. with trace. Westphalian A-B boundary, West Germany.—59. *B. hirsuta*, lower Westphalian A, England.—60. *B. antiqua* with cauline trace (right). Visean, Scotland.—61. *Botryopteris* sp. Herrin Coal, Illinois.—62. *B. mucilaginosa*, lower Westphalian A, Belgium.—63. *B. tridentata.* Mineral Coal, Kansas.—64. *B. ramosa* with pinna trace, lower Westphalian A, England.


A
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foliar system with lower orders of pinnae slightly turned out of the plane of the rachis and clearly planated distal divisions with laminate pinnules (Delevoryas & Morgan, 1954*a*); strongly three-dimensional branching occurs in fertile pinnae complexes and foliar members on shoots at frond bases. Such densely branched non-laminate pinnae are adaxially oriented toward their parent foliar members, and with spatial limitations around the main rhizome (Fig. 65H) the diminutive fronds on lateral shoots at the petiolar bases are extremely compacted. Fertile pinnae complexes are often borne singly at the base of a primary pinna which immediately terminates in a crozier.

Frond branching in *Botryopteris antiqua* (Long, 1943; Surange, 1952; Holden, 1962; Galtier, 1969, 1970), *B. hirsuta* (Long, 1943), and *B. forensis* (Phillips, 1961) shows considerable variation in the relationship of shoots to pinnae. The typical branching patterns involving lateral cauline trace formation may be compared in Figures 65A–D. The variations in *B. antiqua* (Galtier, 1970) include possibilities for deriving the patterns in all the phyletic lines. In *B. antiqua* the shoot is supplied with a cauline trace from a foliar member, and the first petiole is oriented with respect to foliar member bearing the shoot as a pinna would be; in *B. forensis*, except for shoots at petiolar bases, the shoot is similarly derived but at the base of a pinna (Figs. 65D, 73), and its first petiole is also oriented as a pinna. Stratigraphically between the two types are intermediate stages which exhibit a common trace (Figs. 65B–C, 74–75) from a foliar member, resulting in a stem and in a foliar member which may be regarded as either the first petiole of the stem or as the pinna which bears the shoot (Fig. 76).

In the *Botryopteris hirsuta* line, the gross organization does not seem to have changed between *B. antiqua* and *B. forensis*; the "pseudoantiqua" line apparently exhibited the same type of morphological organization, but it is not as well known. Evolutionary changes in the *B. hirsuta* line include lamina development (Galtier, 1970; Delevoryas & Morgan, 1954*a*), changes in pitting from multiseriate scalariform to multiseriate elliptical to circular bordered pitting (Phillips, 1970), and apparently an increase in the overall dimensions of stems and leaves. The largest rhizomes of *B. forensis* are about 1 cm in diameter and frond bases are up to 8 mm wide. Elliptical to circular bordered pitting seems to have occurred geologically in foliar members first; multiseriate scalariform bordered pitting is characteristic of the stems of *B. antiqua* and is regarded as the primitive type in *Botryopteris* as it is in one line of *Tubicaulis* species (Eggert, 1959*b*). Laminate pinnules also occur in the *B. ramosa* line (Fig. 81), and some orders of the frond in the "pseudoantiqua" line developed winged margins (alations) (Fig. 67). Compression specimens of sterile laminate pin-

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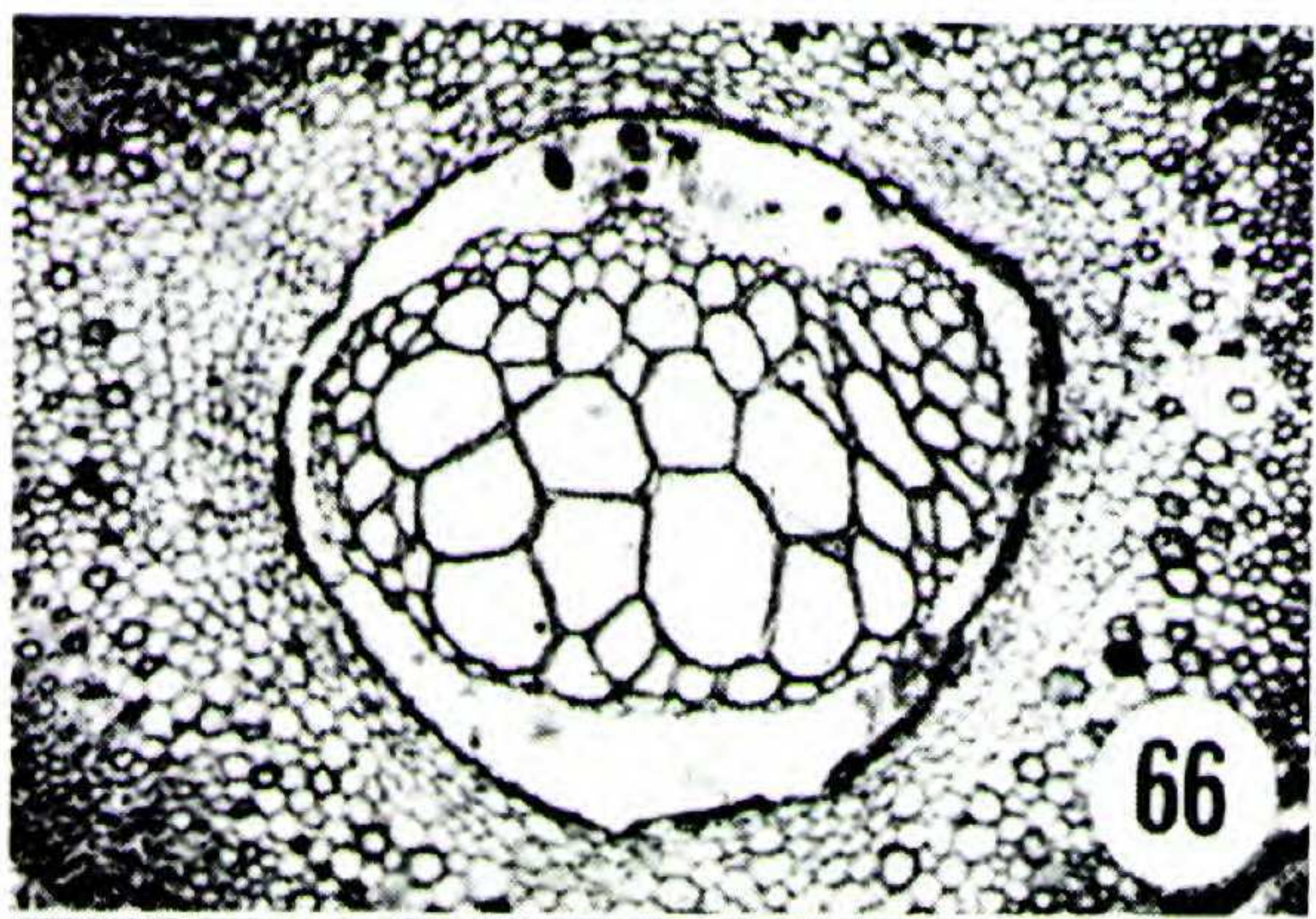
FIGURE 65. Xylary reconstructions of branching in *Botryopteris* with shoots and pinnae on foliar members.—A. *B. antiqua.*—B. *B. hirsuta.*—C. *Botryopteris* sp.—D. *B. forensis.*—E. *B. forensis*, all foliar.—F. *B. ramosa.*—G. *B. tridentata* with siphonostele.—H. *B. forensis* (= *B. trisecta*) with prostrate rhizome bearing three petiolar traces, each with cauline traces or lateral shoots. Drawings modified, in part, from Phillips (1961, 1970).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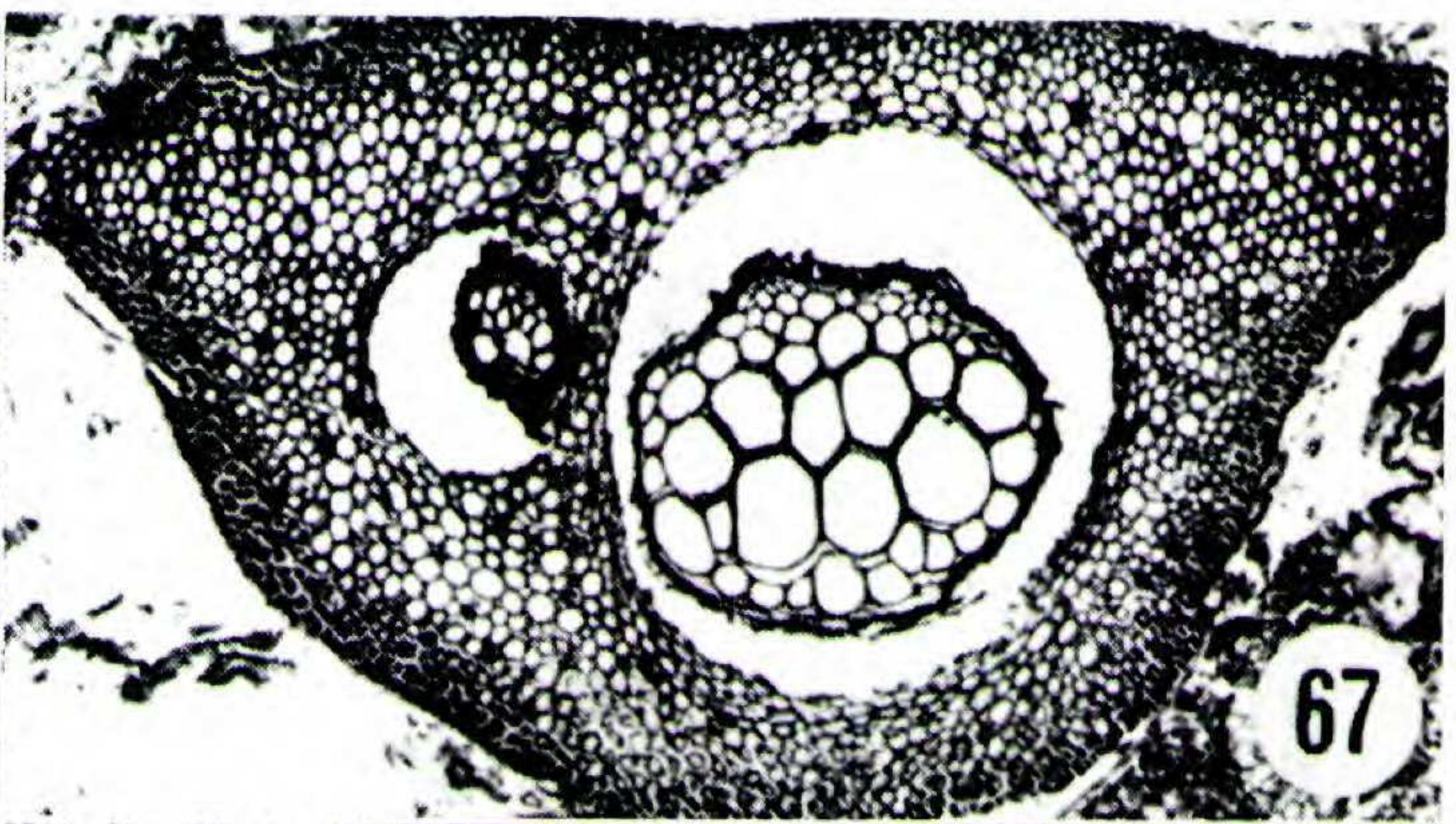
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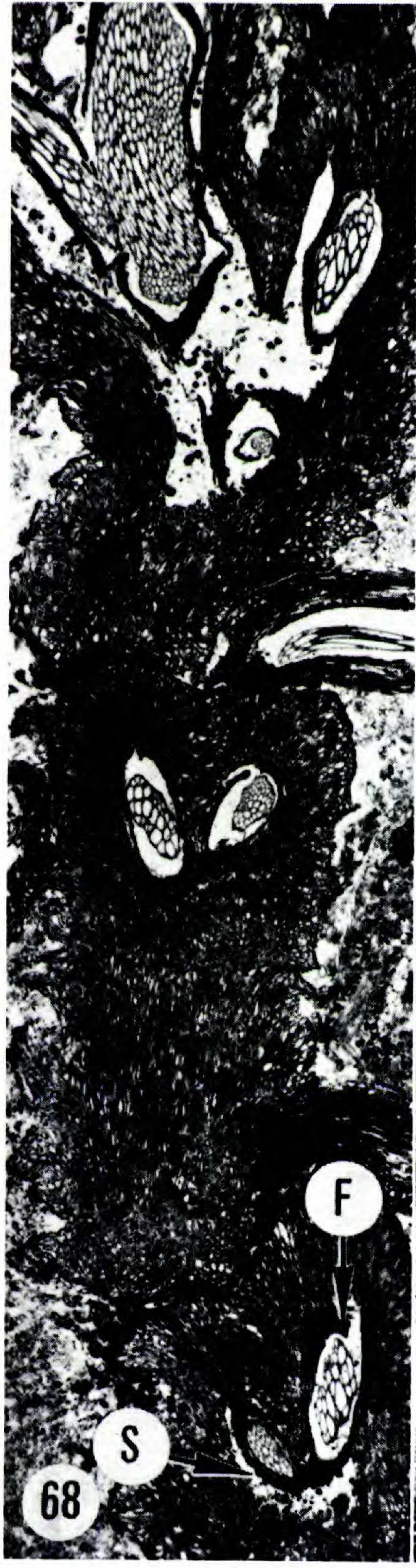

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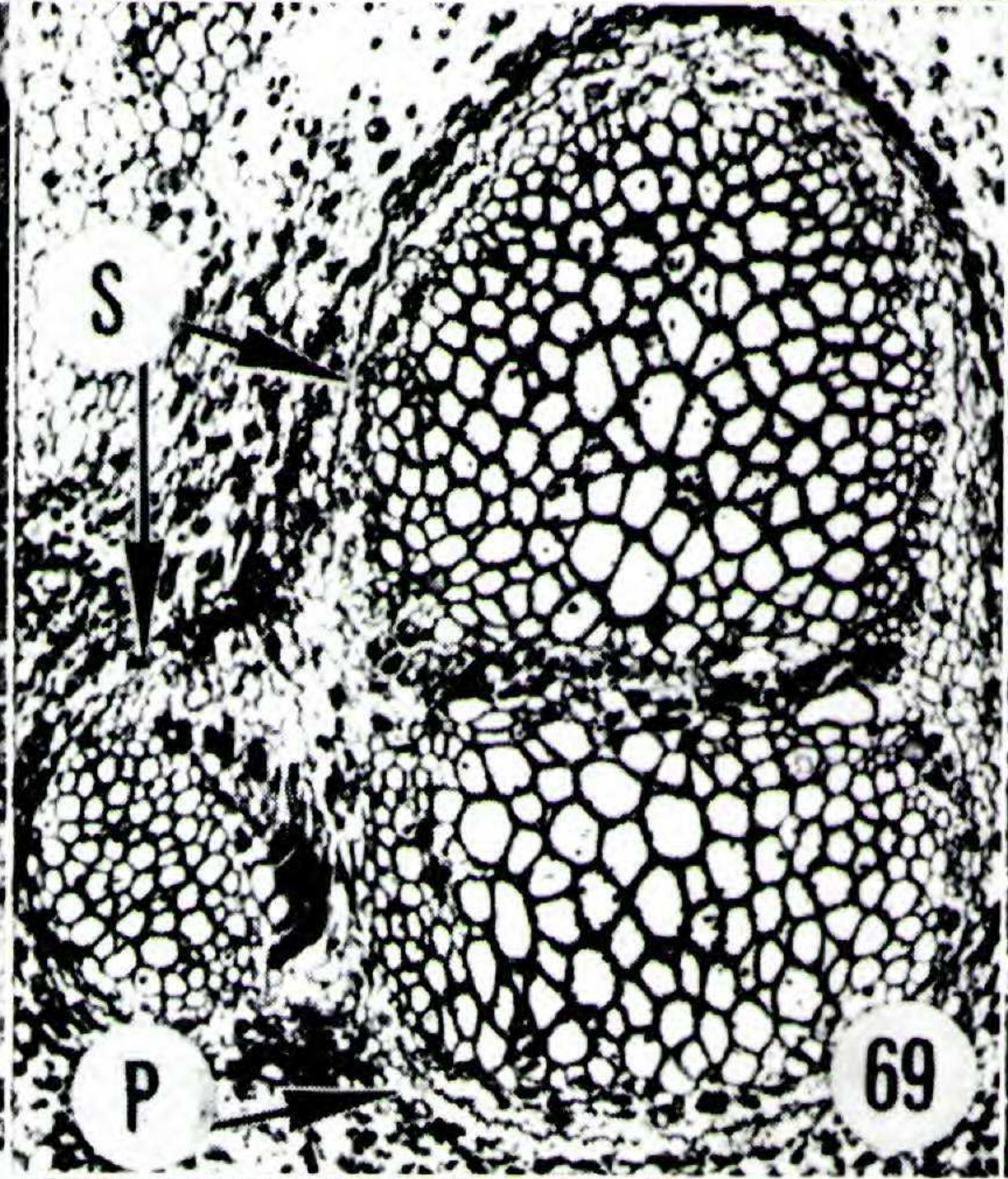

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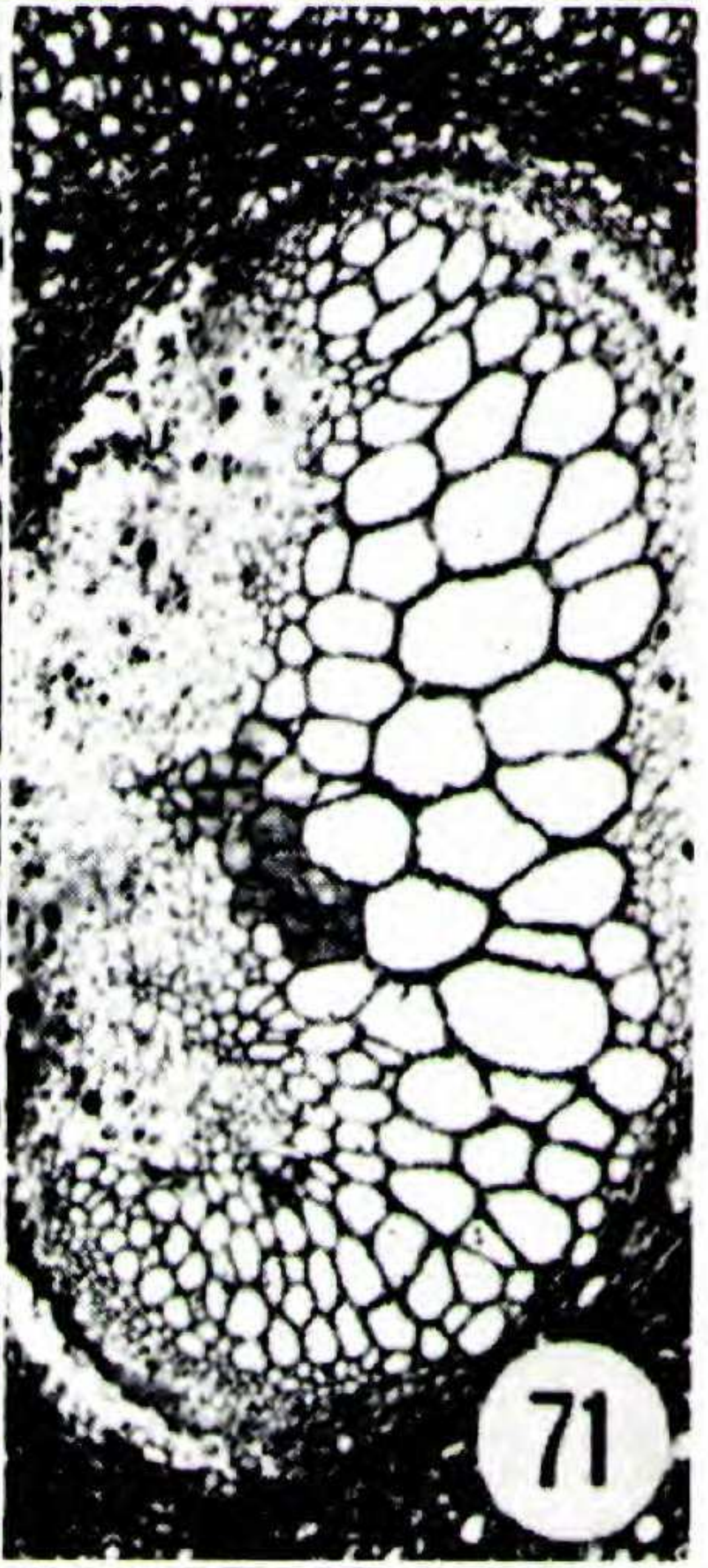
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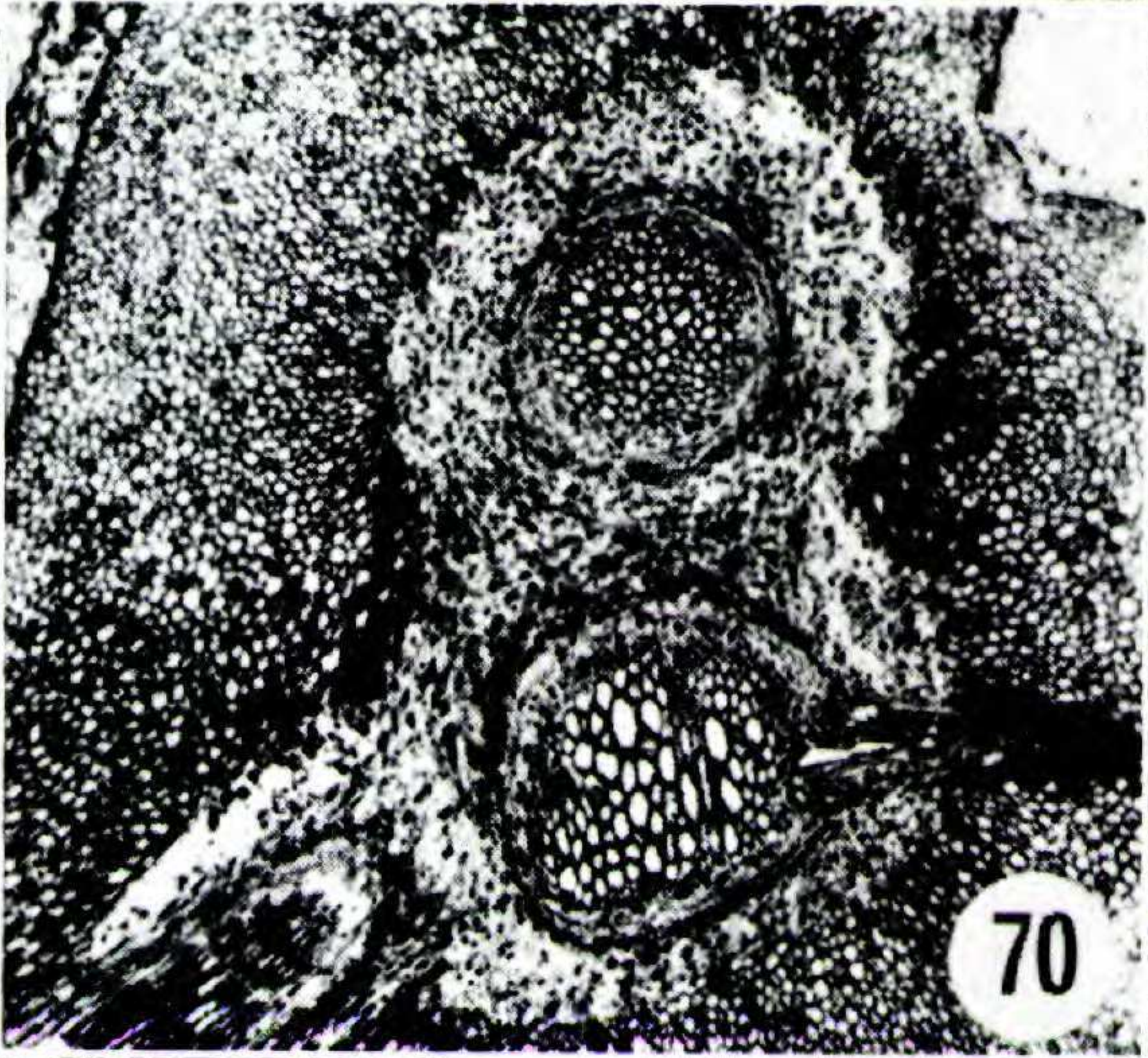
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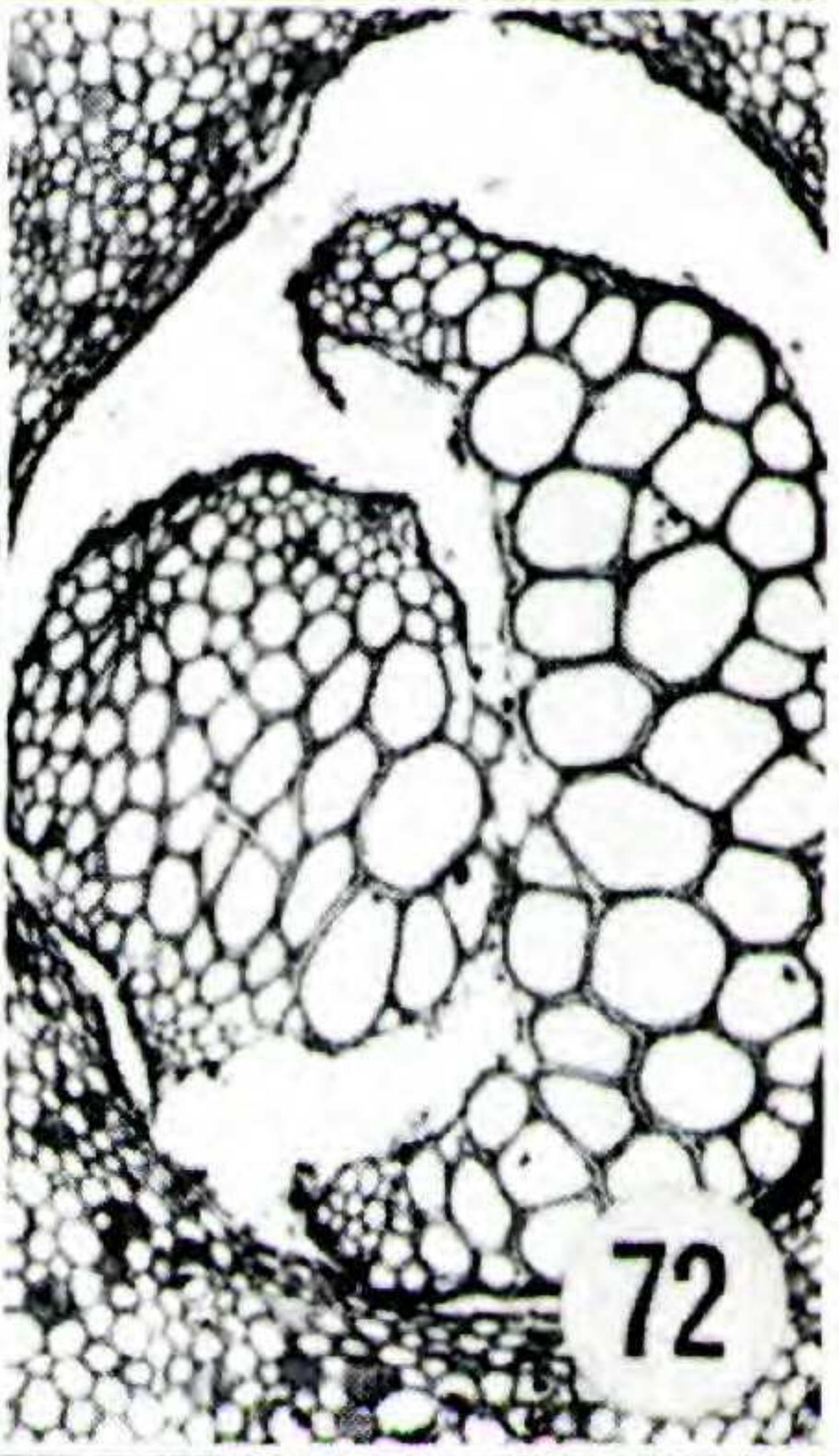
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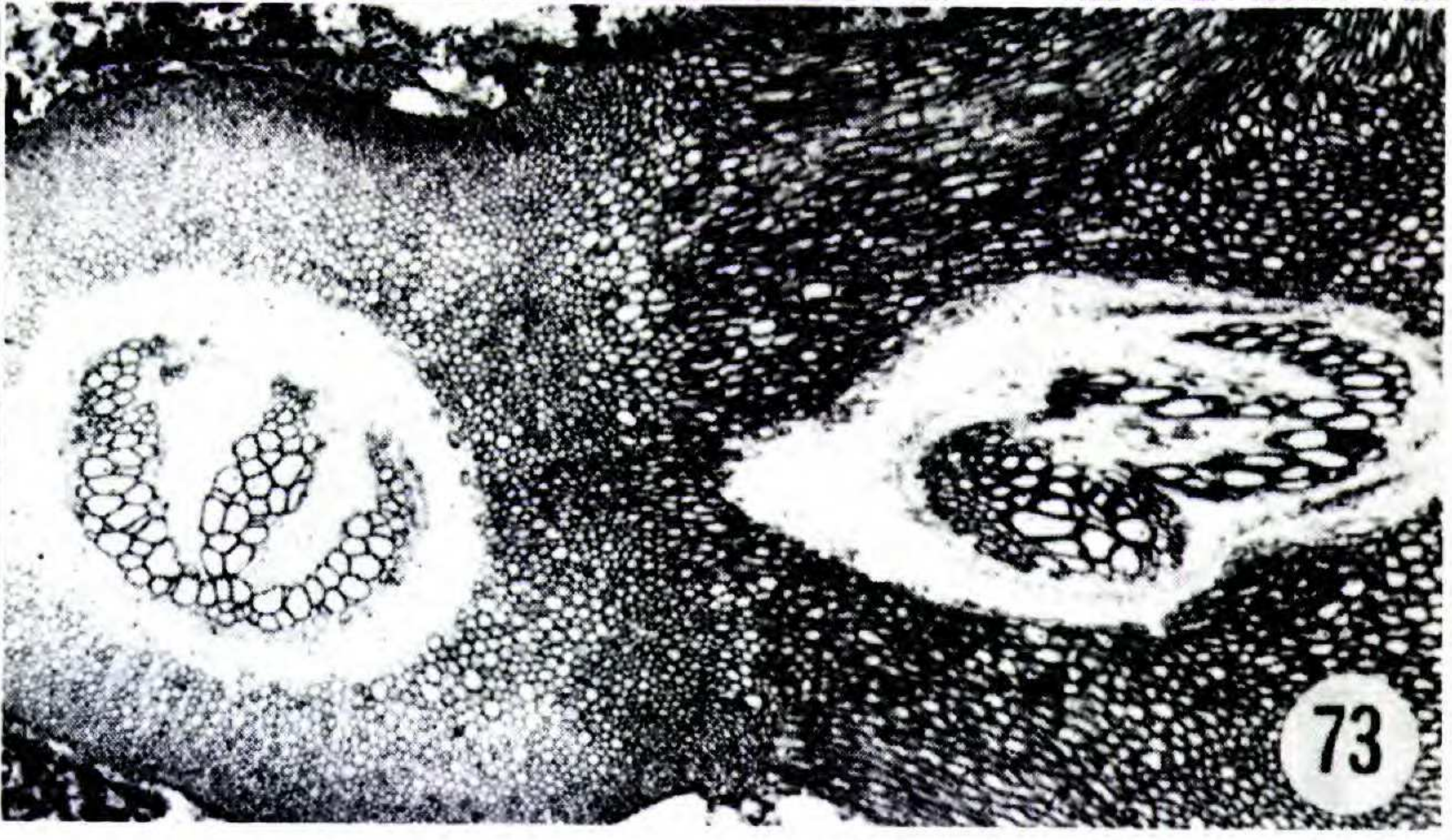
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nules of *Botryopteris* have been reported from the Permian of the Döhlen Basin by Barthel (1970); the foliage is referred to as *Sphenopteris burgkensis*.

Botryopteris stems have terete solid protosteles except *B. tridentata* and bear spirally arranged fronds and diarch roots. The habit in the *B. hirsuta* line (based on *B. antiqua* and *B. forensis*) is a prostrate rhizome with semi-erect apex, as in *Osmunda*, with fronds spaced less closely than in *Tubicaulis*. The same habit is postulated for the *B. ramosa* and "pseudoantiqua" lines. The *B. mucilaginosa* group may have been erect, climbing plants. The stem cortex of the *B. mucilaginosa* line contains distinct clusters of elongate, thick-walled cells with peculiar deposits.

In *B. forensis* (*B. trisecta* of Mamay & Andrews, 1950; Phillips, 1961, 1966) the occurrence of lateral stems on petiolar bases results in a dense "false stem" composed of hundreds of foliar members, their divisions and parent stems around the main rhizome and its fronds (Fig. 65H). This aggregation is up to 15 cm across. In *B. forensis*, *B. antiqua* (Phillips, 1970), and the "pseudoantiqua" line the petiolar traces from the main rhizome (Figs. 68–70) bear one or two lateral cauline traces which in turn bear fronds with compact foliar divisions. Some of the larger lateral shoots may in turn have lateral shoots at their petiolar bases, but this is exceptional.

The evolutionary interpretations of frond morphology in *B. forensis* and the *B. hirsuta* line as a whole are that the frond has evolved from a branch system, having achieved a distinction between cauline and foliar morphology in *B. antiqua*. There has been a progressive planation of foliar branching, achieved in part by *B. antiqua* fronds (Galtier, 1970), and lamination occurred in the *B. hirsuta* stage and was well developed in higher stratigraphic forms (Fig. 57; Delevoryas & Morgan, 1954*a*). The dense, three-dimensional non-laminate branching of fronds on lateral shoots at petiolar bases and in fertile pinna complexes of *B. forensis* may be indicative of primitive branching patterns in forms ancestral to *Botryopteris*. Shoots on fronds throughout the genus probably have evolutionary significance in that the morphogenetic flexibility of apical organization for either foliar or cauline development is consistent with a megaphyllous origin in which the expressions of foliar and cauline morphology are distinct but intermixed. Vegetative propagation is a functional significance of frond-borne shoots in *Botryopteris* as has been suggested in *Anachoropteris* by Hall

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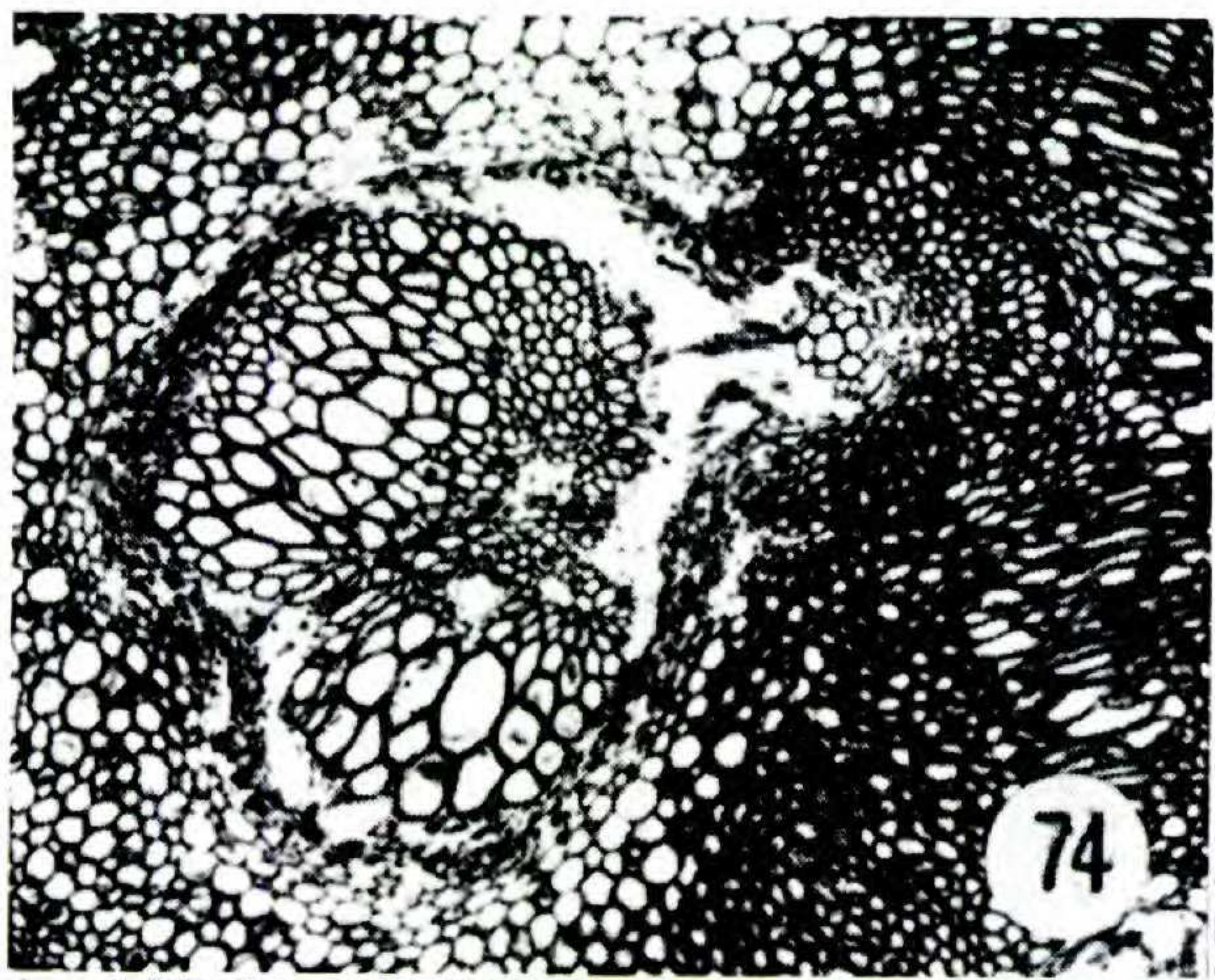
FIGURES 66–73. *Botryopteris* anatomical sections.—66–67. Foliar members of "pseudoantiqua" line. Parker Coal, Indiana and Pottsville Group, Kentucky. × 25.—68. Oblique tangential section of rhizome of "pseudoantiqua" line showing petiolar trace (F) and its lateral cauline trace (S) below and main rhizome stele and petiolar traces at top. Herrin Coal, Illinois. × 10.—69. *B. forensis* (= *B. trisecta*), cross-section of stele of rhizome with petiolar trace (P) and its lateral cauline trace. Cauline steles (S). Calhoun Coal, Illinois. × 10.—70. *B. forensis* (= *B. trisecta*), cross-section of rhizome stele (above) with petiolar trace bearing branch trace (left) and incipient branch trace and root (right). Calhoun Coal, Illinois. × 10.—71. *B. tridentata* foliar member x.s. at level of lateral incipient cauline trace formation. Mineral Coal, Kansas. × 25.—72. *Botryopteris* sp. foliar member x.s. at level of adaxial incipient cauline trace formation. Herrin Coal, Illinois. × 25.—73. *B. forensis*, foliar member (left) with its pinna bearing a cauline trace. Calhoun Coal, Illinois. × 10.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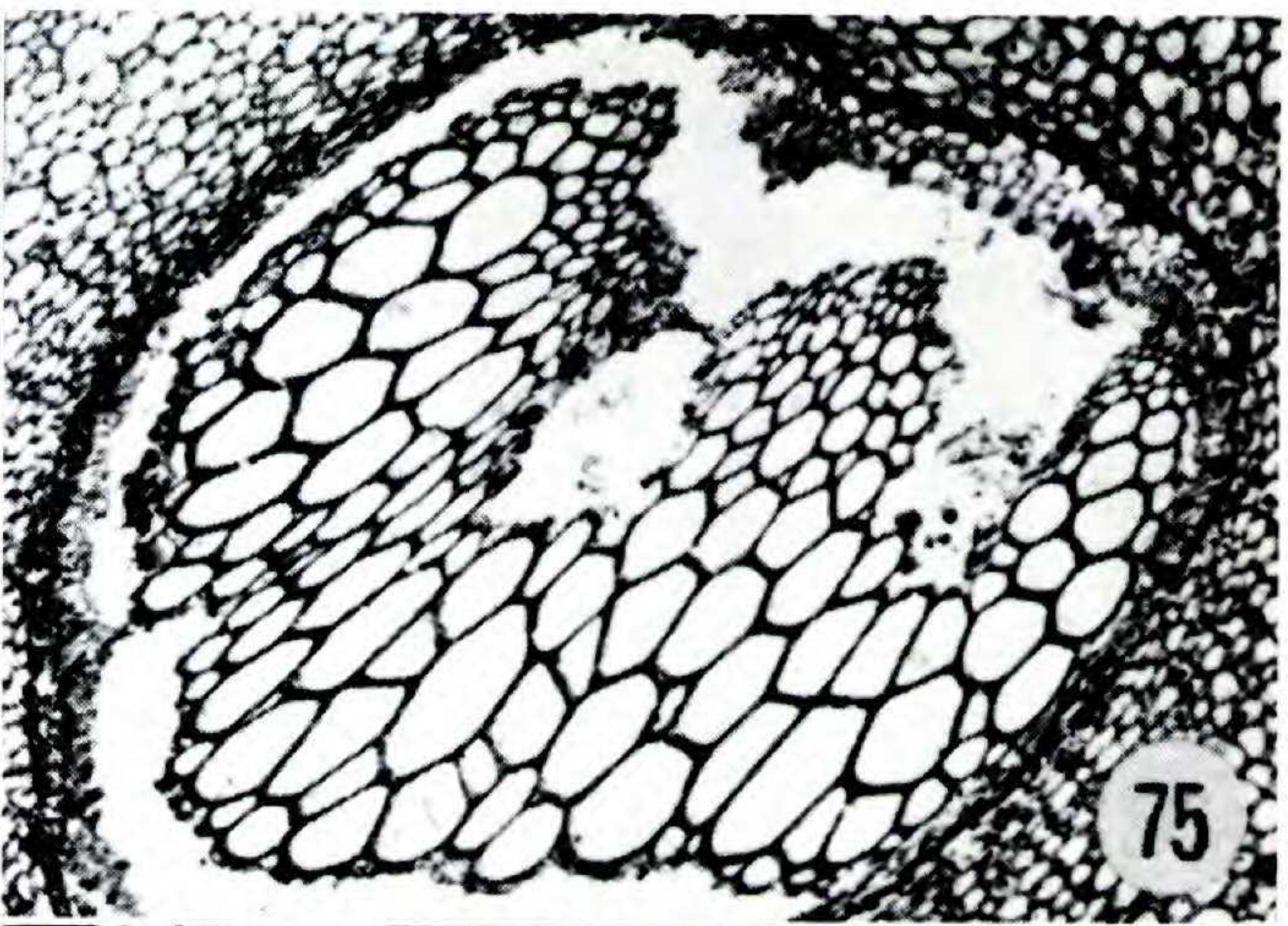
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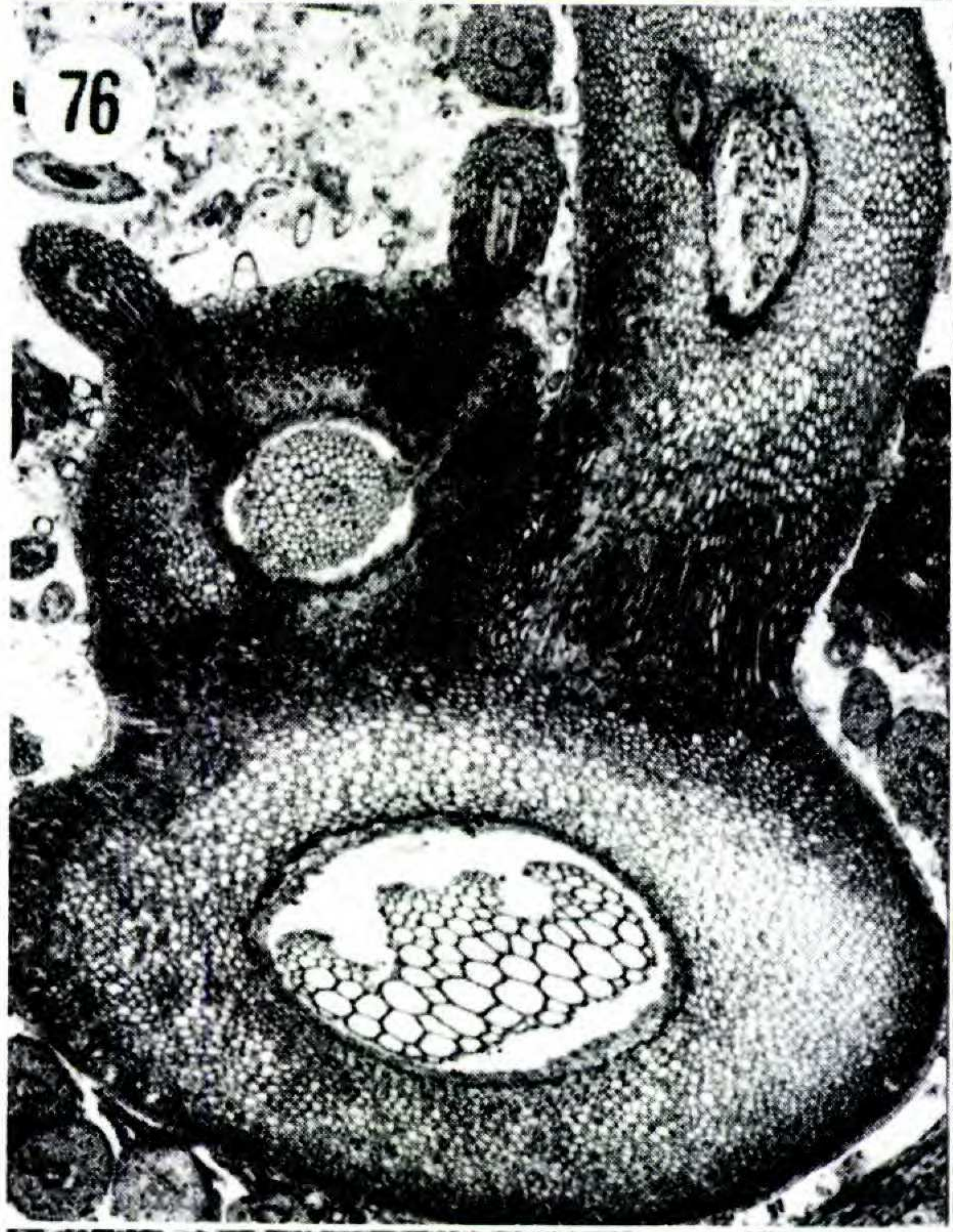
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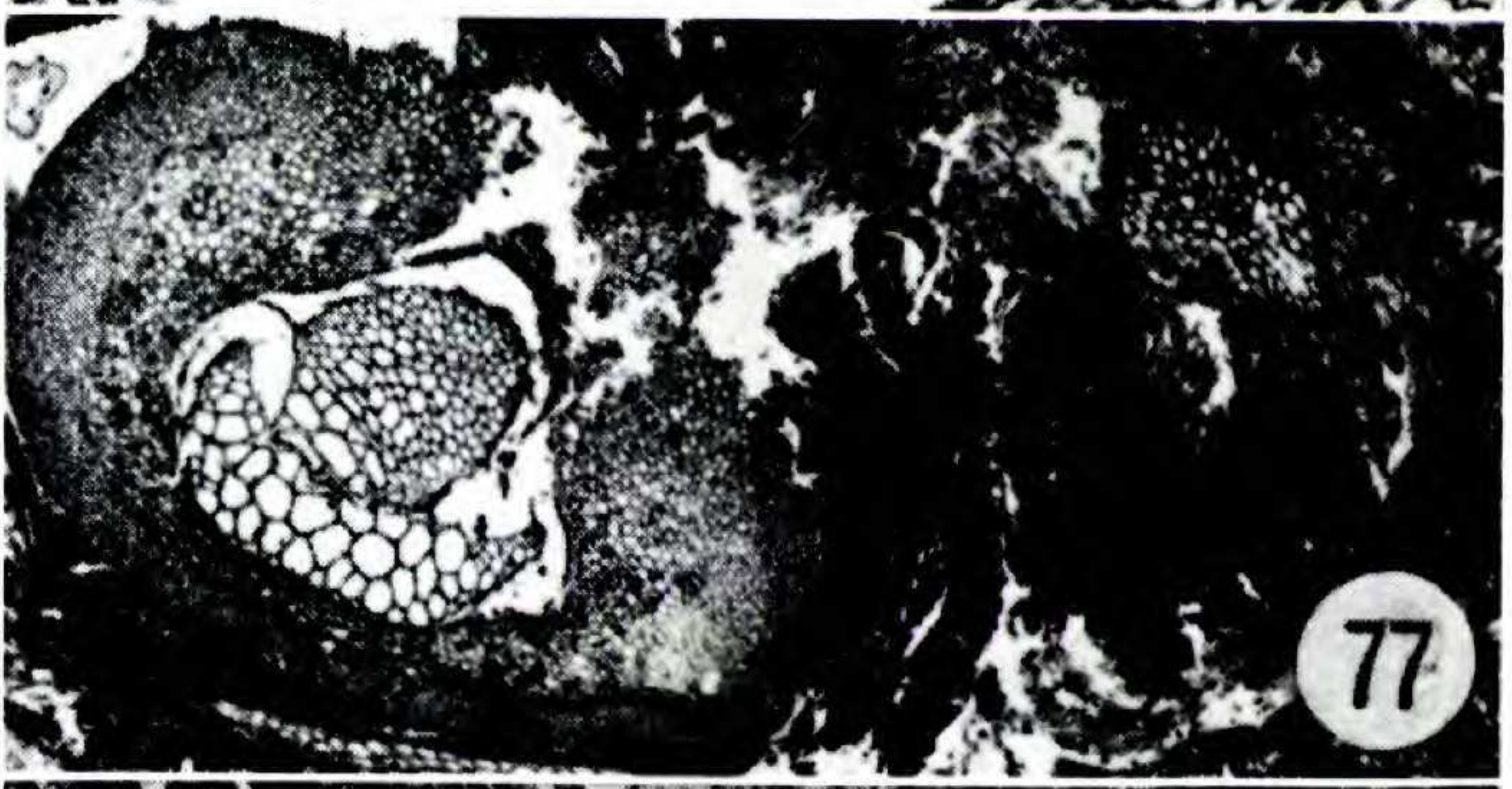
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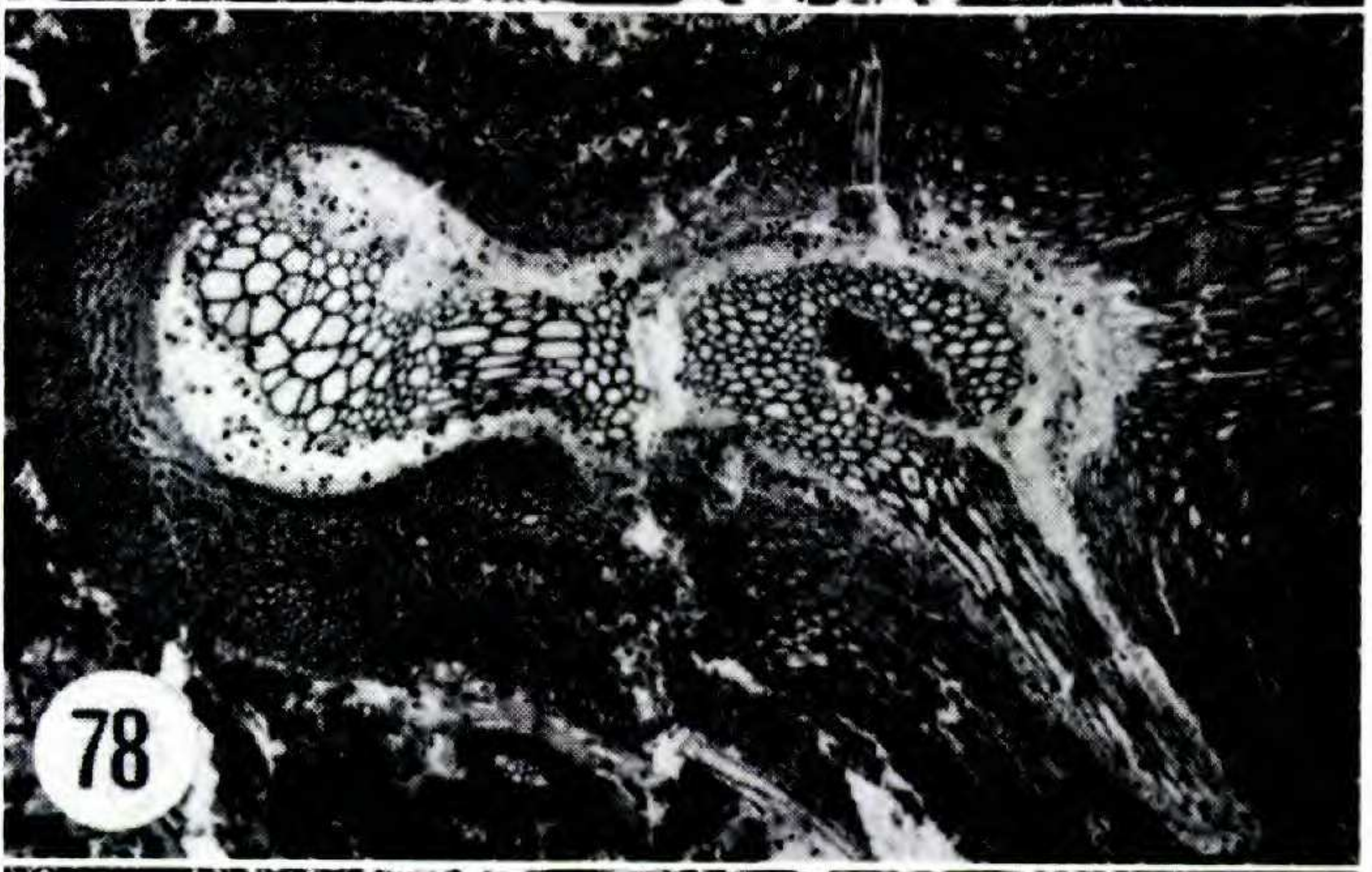
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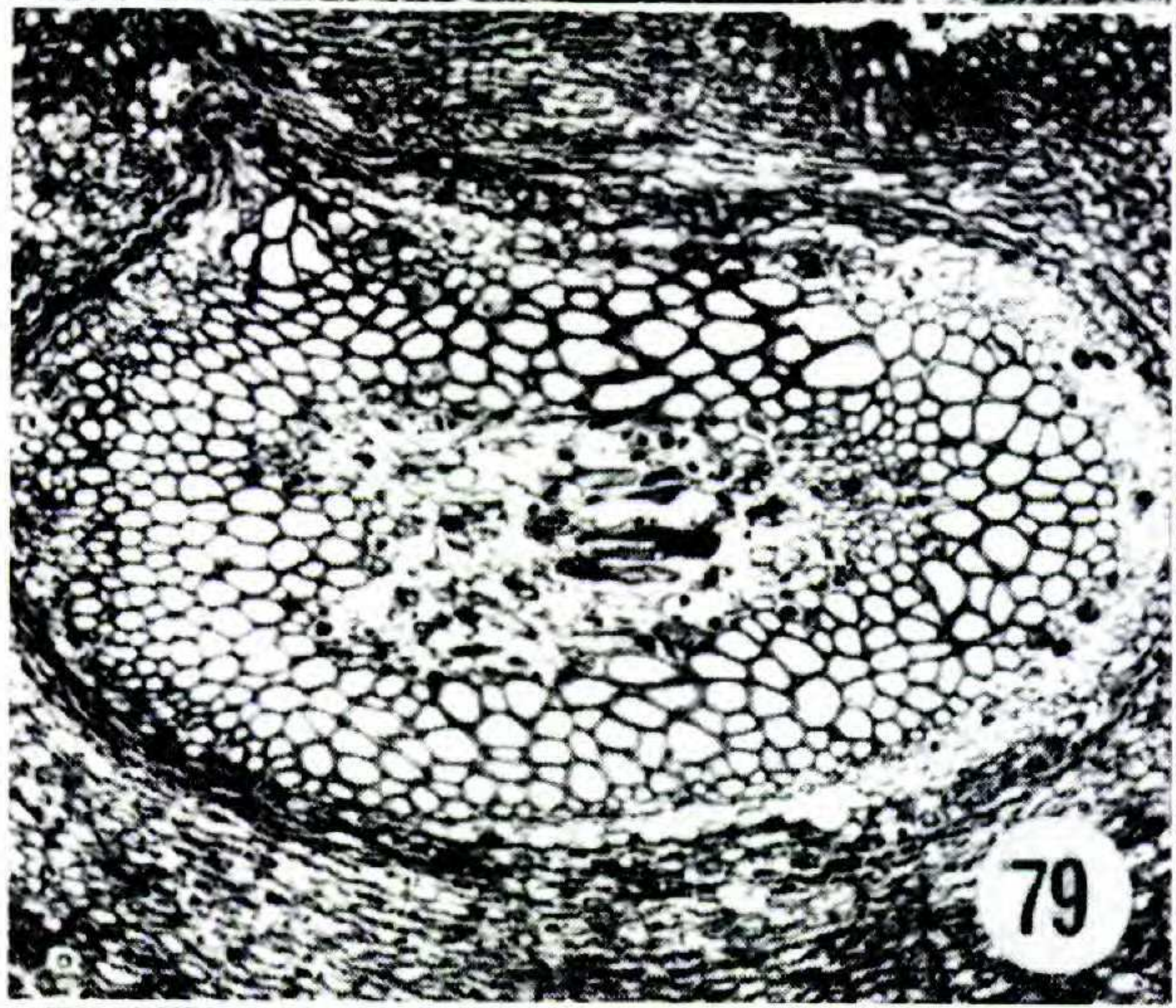
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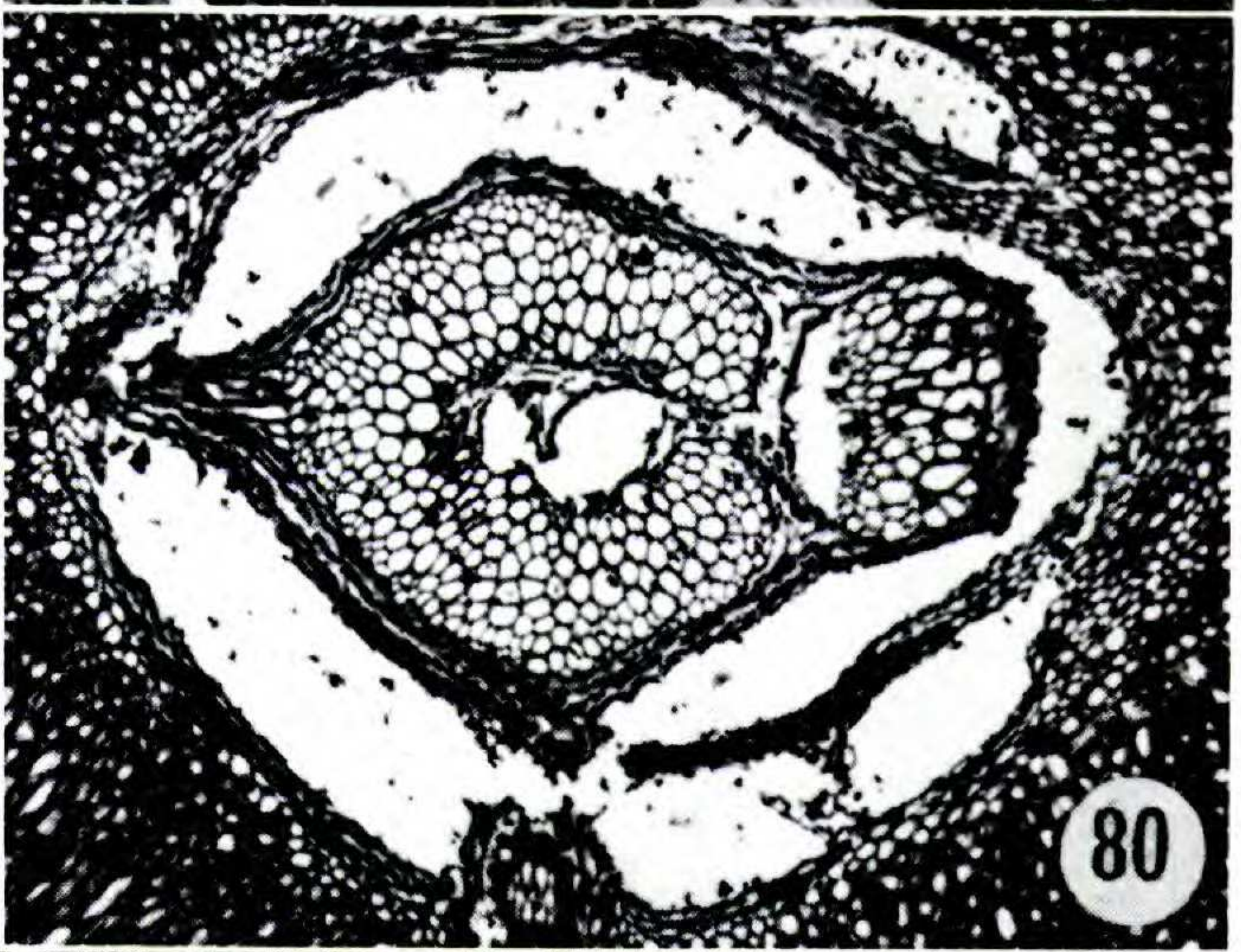
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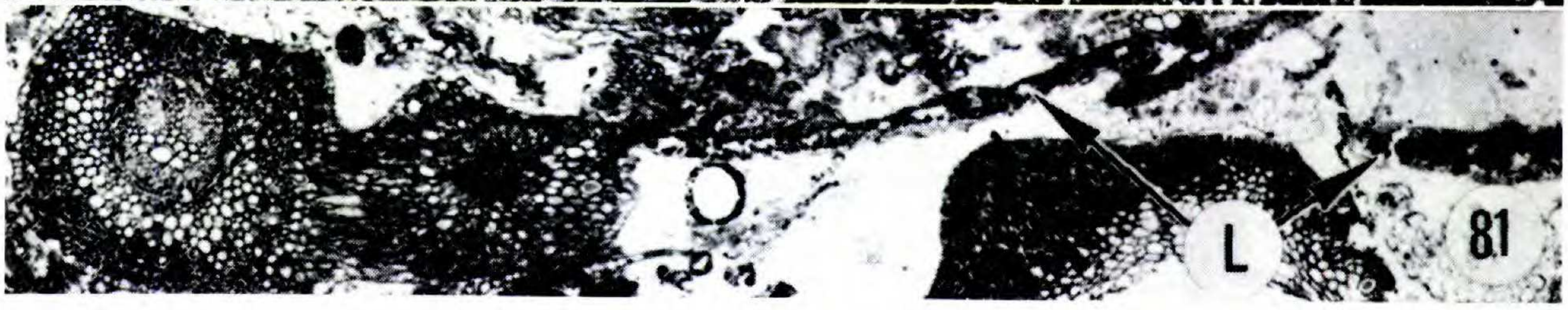
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(1961). Most of the shoots or "buds" on fronds of *Botryopteris*, except those on petiolar bases, and in *Anachoropteris* are small with less than six petioles and with very limited growth except for the basalmost petiole. Such "buds" functioned probably only under conditions of frond damage and/or availability of a rooting substrate. In both genera large (main) rhizomes have developed from such foliar borne shoots (Phillips, 1961; Fig. 53).

The main rhizome is known in each phyletic line except the *B. ramosa* group, and knowledge of cauline anatomy there is exclusively from shoots borne on fronds. Felix (1886) first described the siphonostele of *B. tridentata*, and it was not until comparable American specimens (Fig. 79) were found that his discovery was appreciated as the earliest geologic ocurrence of siphonostely in coenopterids (Westphalian A-B boundary). *Botryopteris tridentata* extends stratigraphically to the Bevier Coal, being particularly abundant in swamp floras rich in cordaites. The siphonostelic trace is formed by a progressive differentiation of tracheids along a lateral foliar arm (Figs. 63, 71) which upwardly arches around to form a circle in which a sclerotic pith appears (Fig. 78); there is no protostelic stage in the foliar-borne siphonosteles. In lower stratigraphic occurrences of *B. tridentata* a few specimens bear protosteles as in *B. ramosa*. Leaf gaps are lacking from many stems, borderline in some (Fig. 80), and clearly present in others. It appears likely that the leaf gap developed after the siphonostele in *B. tridentata* and that leaf gaps and their degree of expression are the result of increasing developmental influences of the frond on stelar differentiation through geologic time. Delicate laminate pinnules with stomata occur in *B. tridentata* by early Middle Pennsylvanian time (Fig. 81).

SUMMARY

The Zygopteridaceae appear in late Devonian time, the Botryopteridaceae in the Visean, the Anachoropteridaceae in the lower Westphalian A and all families extend into the Permian.

Stelar morphology in coenopterid ferns is typically protostelic with solid protosteles in all groups. Vitalized protosteles occur earliest (Visean) in the zygopterid ferns and are the characteristic type. *Zygopteris* exhibits secondary xylem and shows a trend of increased parenchymatization of the protostele between Middle and Upper Pennsylvanian. Vitalized protosteles are not known in the Botryopteridaceae in which evolved the earliest known coenopterid

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FIGURES 74–81. *Botryopteris* anatomical sections.—74. *B. hirsuta*, x.s. common trace at level of distinction between cauline trace (above) and foliar supply, lower Westphalian A, England. × 25.—75. *Botryopteris* sp. Xylem of foliar member with incipient departure of lateral common trace (left). Pottsville Group, Kentucky. × 25.—76. *Botryopteris* sp. Foliar member (below) with attached stem (left) and foliar member from common trace. Pottsville Group, Kentucky. × 10.—77. *Botryopteris* sp. Foliar member (left) with adaxial cauline trace; stem at right, x.s. Herrin Coal, Illinois. × 10.—78. *B. tridentata*, x.s. Foliar member with attached siphonostelic stem bearing a petiole trace. Murphysboro Coal Equivalent, Indiana. × 10.—79–80. *B. tridentata*, x.s. siphonostele with incipient leaf trace formation (Fig. 79) and departure with minute leaf gap. Mineral Coal, Kansas. × 25.—81. *B. tridentata*, pinnae and laminate pinnules (L) x.s. Mineral Coal, Kansas. × 25.

siphonostele (Westphalian A-B Boundary). The Anachoropteridaceae exhibit the most diverse stelar evolution with a general trend toward increased parenchymatization of the mixed protostele, approaching a mixed pith, and the evolution of siphonosteles in both Middle and Upper Pennsylvanian genera. Siphonosteles occur in *Anachoropteris* and *Apotropteris*. Siphonosteles may be transitory or mature features in *Anachoropteris* and occur in larger stems of *Apotropteris*. In both *Botryopteris tridentata* and *Apotropteris minuta* leaf gaps may be present or lacking. Additional evolutionary possibilities are suggested by *Grammatopteris* and *Catenopteris*. Tracheidal zonation with short broad tracheids in the center in *G. baldaufii* may represent a stage leading to a mixed pith or siphonostele as in the Osmundaceae. Corsin's interpretation of *G. rigollotii* could indicate another example of secondary xylem development as in *Zygopteris*. *Catenopteris simplex* with decurrent adaxial parenchyma inserted well into the solid protostele could lead to pith development by an overlap of decurrent parenchyma. The existence of siphonostelic anatomy, leaf gaps, and a catenalean C-shaped foliar xylem strand by early Late Pennsylvanian is indicated by a recently discovered fern from Indiana.

In general, mature secondary thickenings of the metaxylem fall into three categories in the coenopterids. Simple scalariform tracheids occur in the Clepsydroideae, *Ankyropteris* and *Catenopteris*. Multiseriate, scalariform and elliptical to circular bordered pitting occur in the Etapteroideae, Anachoropteridaceae and Botryopteridaceae; the scalariform bordered pitting is considered primitive and the best evolutionary sequence is found in *Botryopteris*.

Roots are diarch.

Cauline branching is predominately dichotomous in the Etapteroideae, axillary in species of *Ankyropteris*, and apparently rare in *Tubicaulis*, *Anachoropteris*, and *Botryopteris*. *Psalixochlaena* rhizomes bear lateral shoots. Shoots occur frequently on fronds of *Botryopteris* and less frequently on *Anachoropteris* fronds. Shoots are borne laterally and adaxially in both genera; shoots also occur by dichotomy of the frond in *Anachoropteris* and at petiolar bases in species of *Botryopteris*. Shoots on fronds were probably important as a means of vegetative propagation and their occurrences in coenopterids are paralleled by modern ferns (McVeigh, 1937), particularly by dennstaedtioid (Arnold & Daugherty, 1964; Troop & Mickel, 1968) and related tropical ferns.

Fronds are biseriate except in the Etapteroideae, and known branching is pinnate except for the primary pinna-pair of the Etapteroideae and certain dichotomous anachoropterid fronds. Planated pinna systems occur in all the coenopterid groups, although there is a common tendency to have primary pinnae (and some higher orders) turned slightly out of the rachis plane. The zygopterids constitute the greatest exception. Repetitive three dimensional branching occurs in some non-laminate fertile pinnae complexes of *Botryopteris* and pinnae on shoots at petiolar bases. Laminate pinnules occur in all familial groups in the Pennsylvanian with identified form genera of foliage including *Pecopteris*, *Sphenopteris*, and *Alloiopteris* (see also Nemejc, 1936).

Aphlebiae and scales are restricted to the zygopterid ferns, and multicellular uniseriate hairs occur in all families.

Coenopterid vegetative morphology supports the increased recognition and appreciation of these Paleozoic ferns as true ferns with distinctions in their cauline and foliar morphology at their earliest presently known stratigraphic occurrences.

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